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THE ORIGIN OF SPECIES

BY CHARLES DARWIN

Annual General Meeting, April, 1959

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The illustration on the cover is from a Wedgwood of Charles Darwin in the Hall of the Society.

Charles Darwin's study at Down House, Kent.
From an engraving by A. H. Haig.

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PENROSE MEMORIAL LECTURE

THE CRUCIAL EVIDENCE FOR HUMAN EVOLUTION

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(*Commemoration of the Centennial of the Publication of* The Origin of Species *by Charles Darwin, Annual Meeting of the American Philosophical Society, April, 1959*)

IT HAS BEEN remarked that it is never possible ultimately to prove a scientific hypothesis—the most that one can hope to do is to disprove it. Except possibly to the more metaphysically minded, this is no doubt an extreme proposition, for plenty of examples could be adduced to illustrate a prediction based on a scientific hypothesis which has subsequently been verified. In the whole field of evolutionary studies, however, the situation is rather different. Here, past events which can never be subjected to direct observation have to be inferred from the data provided by material which is presently existing (even when it consists of relics of the past). In *The Origin of Species* Darwin did of course refer to the geological and fossil evidence for evolution, but at that time he had to stress the imperfection of the geological record, and he realized well enough that critics of his theory of evolution by natural selection would "ask in vain where are the numberless transitional links which must formerly have connected closely allied and representative species." In fact, Darwin's evidence for his theory was derived almost entirely from his observations on living organisms—their variation in nature and under domestication, the tendency of their populations to increase rapidly in numbers and the inference that they are necessarily exposed to what he termed the "struggle for existence," their geographical distribution, and so forth. All this kind of evidence (some of his critics argued), however formidable it might be in its collective and mutual reinforcement, was no more than circumstantial, or presumptive, evidence. Now, it is an interesting question, but one which is not easily answered—just at what point in the gradual accumulation of circumstantial evidence can the latter be accepted as adequate for demonstrating the truth of a proposition? Perhaps the most we can say is that, in practice, this point is mainly determined by the multiplicity of independent sources from which this evidence is derived; if several lines of argument based on apparently unrelated data converge on, and mutually support, the same general conclusion, the probability that this conclusion is correct may appear so high as to carry conviction to the mind of unbiased observers.

In the problem of human evolution, with which Darwin dealt specifically in his *Descent of Man* in 1871, although he had no fossil evidence on which he could rely and could only refer to hypothetical connecting links, he did adduce indirect evidence from a variety of sources which, he wrote, "declare in the plainest manner, that man is descended from some lower form, notwithstanding that connecting-links have not hitherto been discovered." His sources of collateral evidence were derived from comparative anatomy (which demonstrated a unity of design and a close similarity of homologous structures in man and apes), from embryology (which demonstrated that the human embryo passes through phases of early development similar to those found in lower vertebrates, from a consideration of rudimentary elements in the human body (which are unintelligible unless they are assumed to be the relics of fully developed elements which functioned in an ancestral stage of evolution), from a study of human variations (which provide the raw material for evolution by natural selection), and so forth. The cumulative effect of all this evidence was to demonstrate a vast number of facts which were only explicable on the assumption of man's descent from lower forms of life, and to show that, as with animal life in general, natural selection provided the means whereby evolution *could* have occurred. But the evidence that human evolution *did* occur—that is to say the objective and concrete evidence of intermediate stages of evolutionary development in past ages—was yet to be discovered. In a sense, it may be said that Darwin's evidence for human evolution resolved itself into conclusions which were really predictions, that is to say, predictions that in the course of time his conclusions might be

verified by the discovery of the connecting links to which he referred. Indeed, the predictive element in his conclusions was implied in his remark (in *The Descent of Man*): "Nor should it be forgotten that those regions which are the most likely to afford remains connecting man with some extinct ape-like creature, have not as yet been searched by geologists."

We may agree, then, that the verification of Darwin's line of reasoning with regard to the hypothesis of man's descent ultimately depends on the demonstration, by the concrete and objective evidence of actual fossil remains, that intermediate types actually did exist in the past such as he postulated. The facts of comparative anatomy, comparative physiology, embryology, blood reactions, etc., lead to the conclusion that man as we know him today is more closely related to the anthropoid apes than to any other group of living animals. This conclusion is given expression in the now generally accepted scheme of classification which places the human family (Hominidae) in close relationship to the anthropoid ape family (Pongidae); in fact, they are commonly grouped together in the single superfamily, Hominoidea. Such a classification carries with it the implication that, at some time in the distant past, the Hominidae and the Pongidae took their origin from a common ancestral stock and gradually became differentiated by a process of evolutionary diversification. If this is a correct interpretation of the indirect evidence presented by Darwin, we must suppose that, in tracing back the geological record of mankind, we should hope to find in regular temporal sequence a graded succession of types illustrating the evolutionary stages linking modern man with apelike ancestors. This does not mean (and Darwin himself emphasized this point very strongly) that the ancestral stock from which man is presumed to have been derived was similar in all respects to, or even closely resembled, the anthropoid apes which we know today, for the latter are also the terminal products of a long and independent evolutionary process which has led to the development of a number of specialized features peculiar to the modern apes. On the other hand, it may be inferred that the ancestral stock would have been characterized by many primitive characters such as a small brain, retreating forehead, prominent and chinless jaws, and so forth, which later became superseded in the hominid line of evolution by the development of more advanced characters, but which have been retained in the less progressive line of the anthropoid apes.

It is because the final confirmation of Darwin's ideas of the descent of man is only to be found in the fossil record that I refer to the latter in the title of my lecture as the crucial evidence. It is well to emphasize that this evidence, to be valid, must satisfy two requirements. First, it must be able to present a range of fossils showing in their anatomical structure serial gradations which link more primitive with more advanced types. Second, it must be able to demonstrate that these serial gradations are disposed in a regular time sequence—in other words that they represent a real temporal succession of types. Even the Primates of today, that is to say, the order of mammals to which man belongs, can be arranged in a *morphological* "sequence." This was emphasized many years ago by T. H. Huxley in one of his essays in *Man's Place in Nature* (1863), when he remarked "Perhaps no order of mammals presents us with so extraordinary a series of gradations as this—leading us insensibly from the crown and summit of the animal creation down to creatures, from which there is but a step, as it seems, to the lowest, smallest, and least intelligent of the placental mammals." But such a consecutive morphological series, while it carries important implications for the evolutionary argument, does not by itself set the seal to it. The important question is—are these implications confirmed by convincing evidence for an actual temporal succession of an equivalent kind? Since Darwin's time the geological record has indeed supplied much of this more direct evidence in verification of the "predictions" to which I have referred, and it is my intention in this lecture to review the evidence in brief summary.

Let us adventure on a journey backward in time and follow in retrospective order the antecedents of *Homo sapiens* so far as they have been displayed by their fossilized relics. We have not at our disposal any Wellsian time-machine, but we have an excellent substitute for it in the established succession of geological deposits which contain fossilized remains. In recent years the methods and techniques of estimating the chronological order of these deposits have been greatly elaborated, to the extent that their relative dating can often be determined with considerable assurance. This may be done by reference to relative levels of deposits superimposed the one on the other, to the varying thickness of the geological strata (which provides

some indication of the relative length of time required for their deposition), to the succession of climatic changes which are known to have followed in rather regular sequence in different parts of the world and which have left their traces in the soil, and to the slow and gradual accumulation in the fossils themselves of certain chemical elements such as fluorine and uranium. These elements, it may be noted, tend to be taken up by bones which are undergoing fossilization from traces which may be present in percolating waters of the soil, and they accumulate in greater and greater quantity with the passage of time. A chemical analysis of fossils may thus provide important information for their *relative* dating. There are also methods for the determination of an *absolute* dating in terms of years. These methods are difficult of application and they are also limited in the periods of time to which they can be applied. From our present point of view it is particularly unfortunate that they are not (with techniques so far available) applicable to just that period of geological time which evidently saw some of the most significant stages in the evolution of the Hominidae. Thus, the radioactive carbon method permits the estimation of the absolute antiquity of fossils (or associated organic material) not much further back than about 50,000 years. The uranium-helium method, on the other hand, can only be used for estimating the age of much more ancient deposits, and, as far as I am aware, the most recent geological period which has been dated by this method is a stage of the Miocene period, which was about 30 million years ago. But even this distant period has some relevance to our present subject, for it was during the Miocene that many interesting types of primitive and generalized anthropoid apes flourished in the Old World (particularly in the central regions of Africa), and it has been surmised from their anatomical structure that some of these types may have provided the evolutionary material for the subsequent development of the earliest representatives of the Hominidae. Be that as it may, the earliest fossil remains so far discovered which can with certainty be termed "hominid," that is to say, which had already developed anatomical characters which are known to be quite distinctive of the Hominidae as contrasted with the related family Pongidae, occur in geological deposits laid down in the early part of the Pleistocene period. Now, methods of relative dating based on purely geological considerations show a fair agreement that the beginning of this period began somewhere about one million years ago. Obviously, we should like to have estimates of the absolute antiquity of the early hominids which lived during this period, but it will be necessary first to discover some technique similar to the radioactive carbon method which will carry the chronological estimates a long way beyond 50,000 years ago. Until such techniques have been developed, we have to rely for estimates of antiquity during most of the Pleistocene on the methods of relative dating, and it is well to recognize that these methods can only give approximate results.[1]

I may note here that the Pleistocene can be subdivided on a relative chronological basis by reference to its climatic fluctuations. The latter half of the period (or perhaps rather more) was marked by a series of very cold cycles when much of the temperate regions of the earth became covered by glaciers and ice sheets. There were four of these glaciations, separated by three interglacial periods during each of which the climate became much warmer. The last glaciation reached its initial climax probably about 50,000 years ago, and the first glaciation is reckoned to have occurred almost half a million years ago.

Today the family Hominidae is represented by one genus only, *Homo*, and by only one species of this genus, *Homo sapiens*—that is to say, modern mankind. The geographical varieties of this species, or "races" as they are commonly termed, show considerable differences in superficial features such as skin color, hair texture, and so forth, but they are much less easily distinguished by their skeletal characters. Nevertheless, the latter do show differences, and it is well to recognize the extent of these skeletal variations in modern man when the problem arises whether a fossil human skeleton is that of *Homo sapiens*, or of some different and extinct species of *Homo*. For it has happened from time to time, by failing to recognize the wide range of individual and racial variability in our own species, some authorities have claimed that the human remains which they have discovered are those of a hitherto unknown species, and have even christened them with a new specific name. This has had the unfortunate effect of confusing and distorting the perspective of the latter-day prehistory of mankind (so far as it has

[1] The potassium-argon method of absolute dating, which is being currently developed by Dr. J. F. Evernden and his colleagues at the University of California, gives promise of being able to provide absolute ages in the range 50,000–1,000,000 years.

been revealed by fossil remains) to a quite ridiculous degree.

More careful and systematic comparisons have now made it clear that *Homo sapiens* has a quite respectable antiquity. For example, during the time when the Palaeolithic (Old Stone Age) culture known as the Magdalenian flourished in Western Europe, the local population was composed of people who, judging from their skull and skeleton, were similar in physical characters to modern Europeans. The Magdalenians had developed a quite rich culture, and they were responsible for some of the most beautiful examples of cave paintings and sculptures such as those found in the famous caves at Lascaux in France. They lived during the latter phases of the last glaciation in what is sometimes called the Reindeer Age (for the reason that reindeer herds occupied Europe in large numbers at that time). Now, pieces of charcoal left by the Magdalenians in one of the Lascaux caves have been analyzed for their content of radioactive carbon, and this has given an antiquity of about 15,000 years. We can go back further into the Aurignacian period which immediately preceded the Magdalenian, and still we find from a number of fossilized remains that the local population was apparently not distinguishable from modern populations of *Homo sapiens*. A radioactive carbon dating of 27,000 years has recently been reported for the period of the Aurignacian culture, and if the species *Homo sapiens* was already fully differentiated at that time the final stages of its evolutionary emergence must have occurred still earlier. We know also from fossil evidence that the species had spread widely over the earth many thousands of years ago. For example, *Homo sapiens* had certainly reached Australia, and even North America, about 10,000 years ago, and at Florisbad in South Africa there was found in 1933 a human skull, also not to be distinguished from the *Homo sapiens* type, whose antiquity has been estimated by the radioactive carbon method to have been at least 40,000 years.

The question now arises—is there any concrete evidence from the fossil record that *Homo sapiens* was actually in existence before the last glaciation of the Ice Age? Preceding the Aurignacian period in Europe there was a prolonged cultural period of the Palaeolithic termed the Mousterian, which can be conveniently divided into an Early Mousterian phase and a Late Mousterian phase (though this is really an over-simplification of the cultural sequences which followed, and partly overlapped, each other during those times). The Early Mousterian covered the latter part of the last interglacial period and extended into the onset of the last glacial period, while the Late Mousterian coincided with the climax of the first part of the last glaciation. A fair number of fossil remains of Early Mousterian man have been found in Central Europe and also in Palestine, so that we know a good deal about their cranial and dental anatomy. A striking character is their wide variability, for while many individuals show primitive features such as strongly developed brow ridges, a somewhat retreating forehead, prominent jaws, and a feebly formed or absent chin eminence, others are very similar in their skull structure to the more primitive races of modern mankind. Further, the limb bones (so far as they are known) appear to be of quite modern type. Opinions vary on the question whether in some of their skull characters the Early Mousterians exceed the limits of variation found in *Homo sapiens*. Even if this is the case, I myself am not convinced that they exceed the limits to the extent that they can properly be assigned to another species altogether. Probably it is wise to defer a decision on this point for the present—if they are not *Homo sapiens* in the strict sense, they represent the immediate precursors of modern *Homo sapiens* and may be conveniently designated as such. But their great variability is of particular interest from another point of view.

In later Mousterian times, characterized archaeologically by the full development of the typical stone-tool industry to which the term "Mousterian" is properly attached, there existed in Europe and neighboring regions the distinctive type of man now so well known as Neanderthal man. The outstanding features of this type are the massive brow ridges, retreating forehead, large projecting jaws, absence of a chin eminence, and certain peculiarities of the occipital region and base of the skull. Some of the limb bones, also, are unusual in the thickness and curvature of their shafts and the relative size of their articular extremities. In curious contrast, the size of the brain of Neanderthal man—as indicated by the cranial capacity—was surprisingly large, on the average even larger than that of modern *Homo sapiens*. A sufficient number of Neanderthal skulls have been collected to permit of their study by statistical analysis; this has not only demonstrated their homogeneity as a local European

population, it has also shown that in a number of dimensions (and proportional indices constructed therefrom) they lie outside the known range of variation of *Homo sapiens*. All these facts have led to the assumption, maintained by many (but not all) anthropologists, that Neanderthal man constitutes a distinct species, *Homo neanderthalensis*. At one time it was generally supposed that this extinct type was directly ancestral to modern man. But, as I have already mentioned, we now know that it was preceded by earlier types, and these, though showing a number of primitive features, were much more akin to *Homo sapiens*. Moreover, the fossil and archaeological record makes it clear that at the end of the Mousterian period Neanderthal man disappeared from Europe quite abruptly, to be replaced by a population of the modern *Homo sapiens* type. Presumably the latter spread into Europe from a neighboring area, perhaps the Middle East, and by replacement led to the extinction of *Homo neanderthalensis*.

Let us now return to the Early Mousterian populations and reconsider them in the light of their wide range of variability. At one end of this range are individuals which appear to presage the more extreme features of Neanderthal type; at the other end are individuals which approach so closely to primitive races of *Homo sapiens* that it is difficult to decide whether they can be taxonomically separated from this species. In other words, it seems that this degree of variability would readily have provided the raw material, so to speak, for the evolutionary diversification of what were evidently two terminal types—*Homo neanderthalensis* which became extinct, and the modern forms of *Homo sapiens*. Such a conclusion fits in quite well with the evidence relating to the temporal sequence. Some authorities, it may be noted, have been tempted to interpret the variability of Early Mousterians in terms of the coexistence of genetically different types, some of which may have interbred. But this is to complicate the picture unnecessarily and somewhat arbitrarily. The high variability of the Early Mousterians—considered as a single general population composed of regional variants—was probably related to their dispersal over Europe in small hunting communities, their exposure to changing climatic extremes, and the increasing intergroup competition for the means of survival. Such circumstances are particularly favorable for the diversifying action of the selective processes in evolution. It is interesting to note, by the way, that the first Neanderthal skull to be studied—discovered in 1856 in a cave situated in a valley known as Neanderthal (near Düsseldorf)—was discussed at some length by T. H. Huxley in 1863; he expressed the opinion that it was "the most pithecoid of human crania yet discovered," but he concluded that, at the most, it demonstrated "the existence of a man whose skull may be said to revert somewhat towards the pithecoid type." In this statement Huxley showed a remarkable insight, for the accumulation of evidence since his time has certainly made it clear that some of the "pithecoid" features of Neanderthal man were the results of a secondary retrogression. Lastly, it should be mentioned that the Early Mousterians are sometimes referred to as "generalized Neanderthaloids," in contrast to the specialized or "classical Neanderthaloids" which constitute the species *Homo neanderthalensis*.

As far as is known at present, the "specialized Neanderthals," in the strict sense in which this term is commonly used, were limited in their geographical distribution to Europe and certain adjacent areas. But there lived at about the same time, or perhaps rather later, very similar types of prehistoric man in other parts of the world. In Rhodesia and South Africa fossil skulls have been found which also show huge brow ridges and massive jaws, and at Ngandong in Java several other skulls showing the same exaggerated features have come to light. It still remains doubtful what part, if any, was played in the evolutionary history of modern man by the populations represented by these remains. Perhaps they should provisionally be regarded as local variants of *Homo neanderthalensis*—if so, it must be supposed that this species spread very widely over the world in a comparatively short space of geological time. But, in any case, it seems unlikely that they were directly ancestral to the local races of man which now inhabit the regions where they lived (though some authorities have assumed them to be so). Like Neanderthal man in Europe, these aberrant types almost certainly became extinct without leaving direct descendants.

We now come to the problem of "pre-Mousterian man," that is to say, the nature of the populations which immediately preceded the Early Mousterians. Here we are faced with the difficulty that their fossil record is still too meagre to allow firm conclusions. A fairly complete and well-preserved skull found at Steinheim in Germany dates from the last interglacial period, or perhaps

even earlier from the second interglacial period. It closely resembles the Early Mousterians and shows pronounced brow ridges of the skull, but the forehead region is quite well developed and the occipital region is full and rounded as in modern man. The cranial capacity is estimated to be less than 1,100 cc.; this comes well within the range of variation of *Homo sapiens* but is considerably below the mean value (1,350 cc.). Two fragments of skulls found at Fontéchevade in France, also reckoned to be of pre-Mousterian date, show a much closer resemblance to modern *Homo sapiens,* for the brow ridges are only moderate in size. Finally, a most important discovery was made of portions of a skull at Swanscombe in Kent in 1935—important because their antiquity may be assigned with considerable assurance to the second interglacial period which, by methods of relative dating, can hardly have been less than 100,000 years ago and may well have been more. Unfortunately, only three of the main bones forming the roof and back of the skull (the two parietals and the occipital) were found, and although they are excellently preserved they do not tell us very much. But careful anatomical and statistical studies have shown that, while in some respects they are certainly unusual, as far as can be ascertained they do not exceed the range of variation of *Homo sapiens* in their dimensions, shape, and individual structural features. They are unusual in the thickness of the skull wall and in the width of the occipital region. There is also definite evidence that the air sinuses of the face region were extensively developed, and this suggests the probability that the facial skeleton was rather massive, and that the frontal region may have had large brow ridges like the Steinheim skull. Until further remains of the contemporary population are discovered, all we can say, therefore, is that *on the evidence of the three skull bones available* Swanscombe man was probably similar to the Steinheim man, and at least very closely akin to *Homo sapiens.* The brain, incidentally, was quite large (the cranial capacity has been estimated at about 1,320 cc.), and the impressions on the inner surface of the skull bones also show that it was richly convoluted.

In our journey back in time, we have now traced primitive representatives of *Homo sapiens,* or at any rate the immediate precursors of this species, to the second interglacial period, that is to say the Middle Pleistocene. Moreover, there is no structural break in continuity through which these early types are linked in gradational series with modern *Homo sapiens.* If we now continue our journey into still greater antiquity, we come to a period, the early part of the Middle Pleistocene, when a much more primitive type of hominid was distributed over wide areas of the Old World, and at a time when (so far as we can say from the available evidence) *Homo sapiens* had not yet come into existence. So different from *Homo* was this primitive type, and so apelike in certain features of the skull and jaws, that it is usually regarded not only as a separate species of mankind, but as a separate genus, *Pithecanthropus.* The first relics of *Pithecanthropus* to be discovered were found in Java as long ago as 1891. For many years after this, in spite of expeditions which were planned to search for more remains, nothing else was found. Then, in 1937 and the following years, further fossils were brought to light, consisting of a few skulls, some jaw fragments, and a number of teeth. More extensive fossil material representing the same genus has been excavated from caves near Pekin. This was at first regarded as a separate and distinct type and was called *Sinanthropus,* but careful comparisons later made it clear that it is not to be distinguished generically from *Pithecanthropus.* The antiquity of these fossils is very great, but since their age can only be estimated by methods of relative dating, it can only be estimated to a rough approximation—probably somewhere between 200,000 and half a million years. Some of the Javanese representatives of *Pithecanthropus* are more ancient than the Chinese and (as might be anticipated from the time differential) they are in several respects more primitive in their anatomical structure.

Perhaps the most striking feature of the skull of *Pithecanthropus* is the small size of the braincase. The average cranial capacity of all known specimens taken together is only about 1,000 cc., and only about 900 cc. in the Javanese specimens considered separately. The latter actually include a skull with a capacity as low as 775 cc., which is only about 90 cc. greater than the largest so far recorded for anthropoid apes. At the same time, the brain size was evidently very variable, for in one of the skulls from Pekin the cranial capacity reached 1,200 cc., which is well within the range of variation of *Homo sapiens.* Apart from its average small size, the brain case shows a number of other characters which are obtrusively simian. For example, the cranial roof is flattened and the side walls slope downwards and out-

wards so that the brain case as a whole is much broader towards the skull base; the forehead is markedly retreating—indeed, in some skulls a forehead can hardly be said to exist in the ordinary sense of the term; the brow ridges project to form a prominent and uninterrupted shelf of bone overhanging the eye sockets; the jaws are not only massive—they project in muzzle fashion and the lower jaw lacks any trace of chin eminence; the teeth are large, and in some individuals (though this seems to have been unusual) the canines project and partly interlock when the jaws are closed; the occipital region of the skull is marked by strong transverse crests of bone for the attachment of what must have been powerful neck muscles; the nasal aperture is low and broad; and a number of minor features in the construction of the base of the skull also approximate in some degree to the conditions generally regarded as more characteristic of the ape's than the human skull. It is interesting to note, however, that in spite of the lowly appearance of the skull, jaws, and teeth, the limb bones of *Pithecanthropus* are quite similar to those of *Homo sapiens*. Now, this serves to illustrate a most important principle of evolution—that an ancestral species or genus does not become gradually transformed *as a whole* into a descendant species or genus. It commonly happens that different parts or systems of the body evolve at different rates so that transitional stages of evolution show a mosaic of primitive and advanced characters and not an "all round" halfway stage of development. As far as the Hominidae are concerned, it is clear from the fossil record of *Pithecanthropus* that the limbs reached the final stage of their evolutionary development long before the brain, skull, and teeth had done so.

In brief, then, we may picture members of the genus *Pithecanthropus* as rather small-brained individuals with retreating forehead, beetling brows, and big jaws, but with limbs fashioned like our own. But in spite of their relatively small brains they were evidently quite advanced culturally, for we know from the traces they have left of the remains of their feasts and of their cooking hearths that those which inhabited China were skilled hunters and even knew the use of fire. They were also capable of fabricating stone implements, though of a rather crude character. It is of considerable importance for the question whether *Pithecanthropus* could have provided the ancestral basis for the subsequent evolutionary development of *Homo* to note that the remains discovered in the Far East show a fairly wide range of variation. I have already mentioned that the cranial capacity, at its upper limits, reaches close to the mean value of *Homo sapiens*, and there are similar degrees of variability in the size of the jaws, the development of the forehead region, and so forth. In fact, at one end of the range *Pithecanthropus* approaches quite closely to the Early Mousterian or Pre-Mousterian populations which I have already mentioned, and the morphological "gap" between them is almost insignificant. Unfortunately, as has so often happened in the subject of palaeoanthropology, the variants of *Pithecanthropus* have been labelled by different specific or generic names on the unwarranted assumption (or, at any rate, unwarranted on the present evidence) that they actually represent quite different types. There may be some justification for accepting the suggestion, at least provisionally, that the Javanese and Chinese populations represent different species (*P. erectus* and *P. pekinensis*), though even this distinction is doubtful. It is a well-established fact that both the genus *Homo* and also the modern genera of anthropoid apes show a high degree of variability, and if this is duly recognized the variability within the genus *Pithecanthropus* no longer appears exceptional and any further taxonomic subdivision of the genus loses its validity.

It is probable that some local representatives of *Pithecanthropus* persisted in some parts of the world after the evolutionary appearance of the genus *Homo* in other parts, but the fact remains that the earliest representatives so far known appear to have preceded the appearance of *Homo*. Thus the temporal sequence fits in with the evidence of the graded morphological series which they present, and supports the proposition that the one was probably ancestral to the other.

The most abundant remains of *Pithecanthropus* which have been discovered are those of the local populations which lived in the Far East, but there is now fossil evidence that this ancient type was by no means confined to that region of the world. For example, there have recently been found in Algeria three fossil jaws and a parietal bone of the skull which so closely resemble those of Pekin man that they are not really distinguishable in the generic sense. In spite of this, these remains have been given a new name, *Atlanthropus*, an appellation which is unfortunate not only because it seems unjustified, but also because it introduces an unnecessary complication and may obscure their real significance for human evolution. These Algerian

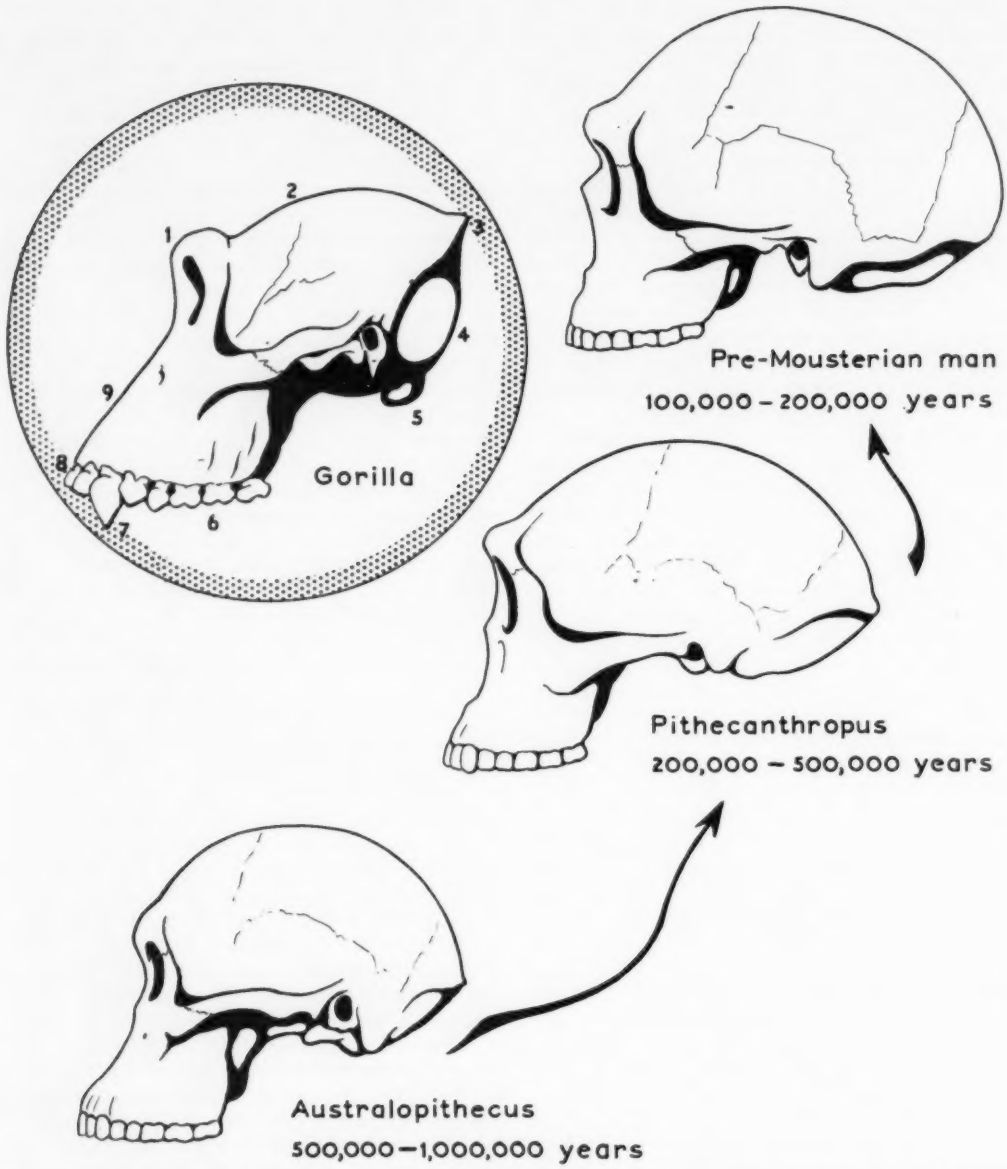
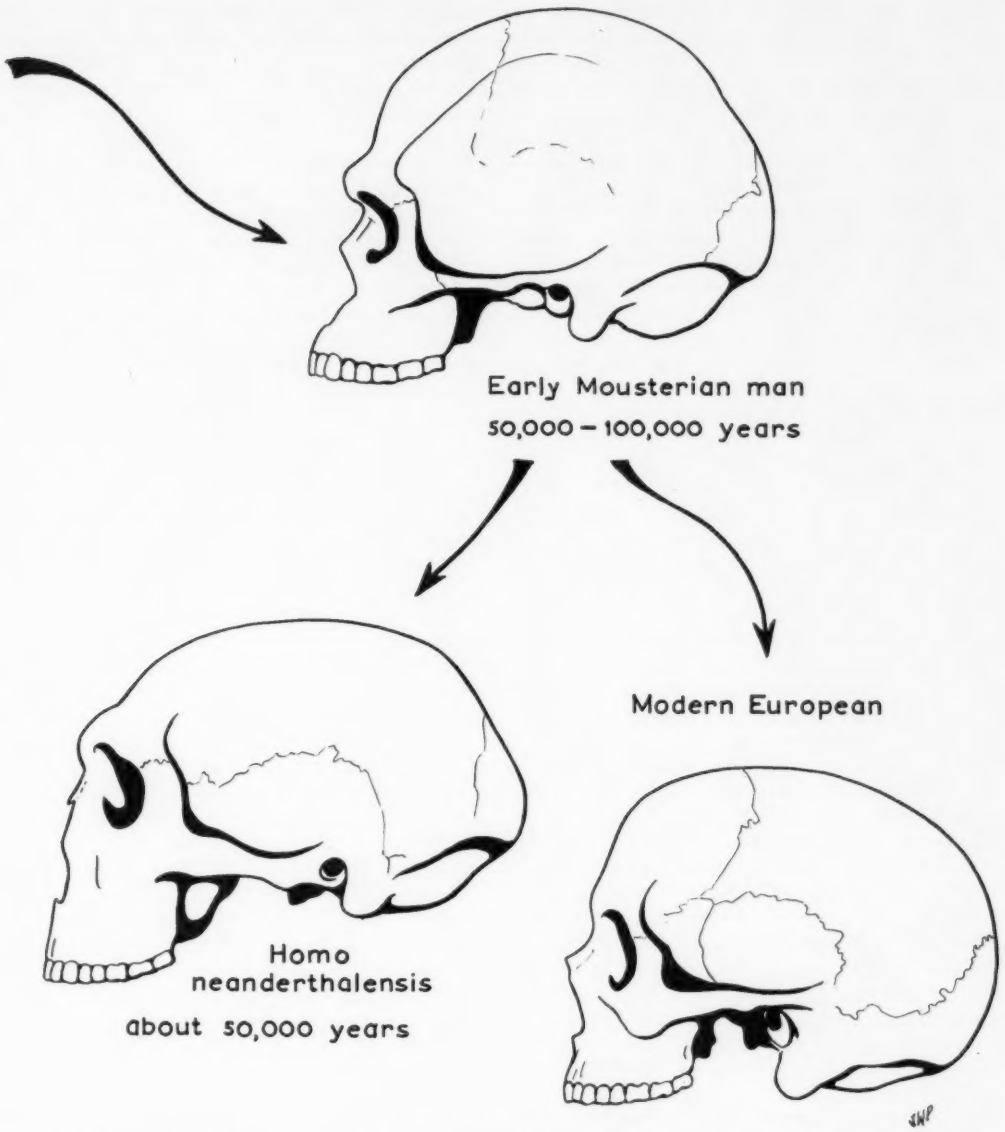


FIG. 1. This diagram illustrates the appearance of the skull in a series of fossil hominid types arranged in their temporal sequence. The antiquity of each type has been estimated by methods of relative dating and is to be regarded as no more than approximate within very broad limits. It is also to be noted that some of these types overlapped in time in different geographical regions. The representation of the genus *Australopithecus* is based on a skull found at Sterkfontein in South Africa, *Pithecanthropus* on a skull cap and portions of jaws found in Java, pre-Mousterian man on the Steinheim skull, Early Mousterian man on one of the skulls found at Mount Carmel in Palestine, and Neanderthal man on a skull found at Monte Circeo in Italy. Inset on the left is shown, for comparison and contrast, the skull of an adult female gorilla; the numerals indicate a few of the fundamental characters which, *taken in combination*, comprise a total morphological pattern distinguishing the anthropoid ape type



of skull from the hominid type of skull. The characters indicated are: (1) The forward projection of the brow ridges well beyond the front end of the brain case. (2) The low level of the cranial roof in relation to the upper border of the orbital aperture. (3) The high position of the external occipital protuberance. (4) The steep slope and great extent of the nuchal area of the occiput for the attachment of the neck muscles. (5) The relatively backward position of the occipital condyles. (6) Except in advanced stages of attrition, the teeth are not worn down to a flat, even surface. (7) The canines form conical, projecting, and sharply pointed "tusks." (8) The large size of the incisor teeth. (9) The massive upper jaw. Note, also, that in the hominid type of skull a pyramidal mastoid process of quite distinctive pattern is consistently present.

All the skulls have been drawn to the same scale, one third natural size.

remains were found in association with stone implements referable to the Early Acheulian phase of Palaeolithic culture, and there is reason to suppose that they date from the early part of the second interglacial period, probably more or less contemporaneously with the later Javanese fossils but antedating Swanscombe man. Another possible representative of *Pithecanthropus* is "Heidelberg man," known only from a massive lower jaw discovered in 1908, and probably of somewhat greater antiquity than the Algerian fossils. But the dentition of this species shows certain features which have led some authorities to think that its relation to *Pithecanthropus* may not be very close. Obviously, a decision on this question can only be reached when further fossil material of Heidelberg man is available for comparative study.

Thus far, it seems, we have a fossil record which, though still by no means as well documented as we could wish, does suggest a high degree of probability that from the beginning of the Middle Pleistocene onwards there has been a progressive sequence of hominid types leading almost insensibly from the primitive, small-brained *Pithecanthropus* through pre-Mousterian and Early Mousterian man to *Homo sapiens* as this species exists today. If Darwin's line of reasoning from the indirect evidence at his disposal is sound, it might be predicted that the genus *Pithecanthropus* would itself have been preceded by a type showing even more primitive and ape-like features, such as a still smaller brain, jaws of more simian dimensions, and so forth. Until 1924, we had no direct knowledge at all that any such connecting link had actually existed. In that year there was found a remarkably fine and well-preserved specimen of a new type of hominid which conformed in a most remarkable way with expectations and thus, once again, provided a verification of the predictions implied by less direct evidence. In more recent years great quantities of the fossilized remains of these creatures have been collected from cave deposits at widely different sites in the Transvaal, so that it is possible to speak with considerable assurance about their anatomical characters. Of the latter, undoubtedly the most striking is the size of the brain case, for this is not only much smaller when compared with *Pithecanthropus*, it actually overlaps the range of the modern large apes. The small brain case, combined with huge jaws, gives the whole skull a very simian appearance indeed, and it was for this reason that on their first discovery they were given the name *Australopithecus* (which means the "southern ape"). As we know now, however, they were not apes in the strict taxonomic sense of zoological nomenclature; they were exceedingly primitive hominids which in a number of fundamental features had already developed a considerable way along the direction of hominid evolution and quite opposite to the direction of evolution which characterized the anthropoid ape family (Pongidae). In fact, they provide another excellent example of "mosaic evolution" in their combination of relatively advanced hominid features with the continued retention of primitive features inherited in common with the Pongidae from a common ancestral stock. The range of variation of the cranial capacity in *Australopithecus* has not been determined with any certainty; most of the skulls so far discovered are too incomplete, or distorted by crushing, to allow of direct estimates. Probably, however, they ranged from about 450 cc. up to about 700 cc. The higher estimates of much over 700 cc. which have been suggested for some of the specimens are too insecure to be reliable, and it is likely that they are overestimates.

It is perhaps not surprising that the earlier reports of these South African fossils were received with some scepticism and gave rise to a good deal of controversy. Because of the intense interest which they arouse, it seems almost inevitable that every discovery of fossil hominids which appears to confirm Darwin's anticipation of connecting links should be followed by controversies, and these have often been of rather a contentious and polemical character; indeed, opposing views still tend to be expressed with a vehemence which is rather unusual in scientific discussions today. No doubt this is to be explained by the fact that the problem of our own origin is by its very nature a peculiarly personal problem, so much so that even scientists may sometimes find it difficult to free their minds entirely of an emotional bias and to view the evidence quite dispassionately. In the case of *Australopithecus*, it has been the distinctively hominid characters which formed the main center of controversy, for the obviously primitive (and therefore ape-like) general proportions of the skull have never been in dispute. Let me enumerate some of the most fundamental of these hominid characters very briefly, in order to emphasize their significance for the correct interpretation of the evolutionary position of *Australopithecus*.

In their evolutionary divergence the ape line of development and the hominid line have followed

in many respects very different trends. Of special significance are the contrasting trends in the dentition, for experience has shown that the comparative anatomy of the teeth can often provide particularly reliable evidence for the assessment of evolutionary affinities. In the anthropoid ape sequence of evolution, for example, the front teeth (incisors) have increased in size (leading to a broadening of the front of the jaws); as a result, the grinding teeth become disposed in rows which are parallel, or even diverge anteriorly; the canine teeth have formed powerful and projecting tusks which interlock when the jaws are closed; there is almost always a pronounced gap (diastema) in front of the upper canine to allow room for the interlocking lower canine; the front lower premolar tooth (immediately behind the canine) has accentuated the pointed and cutting (sectorial) character which is commonly found in lower Primates. In the course of hominid evolution, on the other hand, the incisor teeth remain relatively small; the dental arcade becomes evenly curved in parabolic form; the canine teeth have dwindled in size and assumed a spatulate shape—they do not project or interlock and they lie in uninterrupted series with the incisors with no abrupt contrast in their size and shape; there is normally no diastema; the front lower premolar tooth assumes a non-sectorial, bicuspid shape. In every one of these fundamental characters *Australopithecus* conforms to the hominid pattern of the dentition. The differences from the pongid type of dentition are sufficiently abrupt and clear-cut to be readily apparent simply by direct visual comparison, but they have also been abundantly confirmed by statistical analyses.

When the first australopithecine skull was found, attention was called to certain, not very conspicuous, features in which it appeared to approximate to the hominid type of skull. Later discoveries considerably reinforced the inferences drawn from these similarities, in particular an adult skull, complete except for the lower jaw and unusually well preserved, excavated in a cave at Sterkfontein near Johannesburg. This exceptional specimen has provided the opportunity for making satisfactory comparisons with extensive series of ape's skulls, and has thus served to demonstrate some rather impressive contrasts. For example, the height of the brain case in relation to the eye sockets exceeds the range of variation found in any of the apes, and so does the low position of the muscular ridge on the back of the skull for the attachment of the neck muscles. Similarly, the relatively forward position of the occipital condyles on the base of the skull (for articulation with the upper end of the vertebral column) indicates a significant approach towards the hominid condition. Together with other characters of the skull such as the conformation of the articular socket for the condyle of the lower jaw, certain structural details of the lower jaw, and the consistent presence in all the known skulls (young as well as adult) of a prominent mastoid process of typical human shape, all these anatomical details comprise a total pattern of construction which is not found in ape skulls, but which is found in hominid skulls. Thus, in spite of the simian appearance of the *general* proportions of the skull, the structural details of the latter add further support to the evidence of the dentition that the australopithecines represent an early phase in the hominid sequence of evolution.

On the basis of the early discoveries, it had been inferred from some of the features of the skull base that the australopithecines quite probably were erect, bipedal creatures, for these features appeared to indicate that the head was poised more or less evenly on the top of a vertical spinal column, and not held up by powerful neck muscles on a forwardly sloping spine as it is in apes. This indirect evidence could not by itself, of course, amount to a final proof of erect bipedalism; while it certainly justified a strong presumption that such was the case, it was at that time no more than predictive and therefore depended for its corroboration on the accession of more direct evidence. In fact, confirmatory evidence was later supplied by a detailed study of the thigh bone, and the earlier predictions finally received the most remarkable verification when specimens of the pelvis were found. Now, there is no element of the skeleton which is more distinctive of the Hominidae as compared with the large apes than the bony pelvis. In the two families it has very different proportions, which are evidently associated mainly with radical differences in posture and gait. Altogether, four different specimens of the australopithecine pelvis have been found at widely different sites in South Africa, and they all conform in their fundamental characters to the hominid pattern of construction. There can be no reasonable doubt, therefore, that the australopithecines had already achieved an erect, bipedal posture. But it should be emphasized that the pelvis shows certain differences in detail from that of *Homo sapiens*, and it may be assumed from a consideration of these

differences that they had not developed the erect posture to the perfection found in modern man.[2]

When the first pelvis of *Australopithecus* was found its hominid character appeared to be in such startling contrast to the small brain of these creatures that some doubt was felt whether it actually did belong to *Australopithecus* (and not, perhaps, to some more advanced type of hominid which may have lived contemporaneously in the same region). However, apart from the fact that further excavations now appear to have eliminated this possibility, it seems that those who felt incredulous at the first discovery perhaps did not realize how common is the phenomenon of mosaic evolution, or that this phenomenon must be presumed to apply to hominid evolution in the same way that it does to that of other groups of vertebrates. After all, we know that at the *Pithecanthropus* stage of hominid evolution the limbs had already reached their final development while the skull, jaws, and brain still retained very primitive characters. From this evidence alone it might have been anticipated that the precursors of *Pithecanthropus* would show indications of a differential development of a similar type, that is to say, that the limbs would already have advanced along the hominid direction of evolution beyond the level reached by the skull, jaws, and brain.

Morphologically speaking, the genus *Australopithecus* conforms so closely to theoretical postulates for the connecting link which must be presumed to have been immediately ancestral to *Pithecanthropus*, that a true ancestral relationship seems extremely probable. The important question arises whether this inference fits into the time relationships. As the result of intensive studies of the australopithecine deposits in South Africa based on several collateral lines of evidence, it now appears certain that the most ancient remains of *Australopithecus* so far discovered did antedate *Pithecanthropus*. As I have already mentioned, the earliest representatives of *Pithecanthropus* probably date back to the beginning of the Middle Pleistocene.[3] *Australopithecus* in South Africa on the other hand, dates back to the Early Pleistocene, and it may therefore have an antiquity greater by some hundreds of thousand years. No doubt we must await further evidence for a conclusive statement on the relative time spans of *Australopithecus* and *Pithecanthropus*, but at least as far as our present information goes the inference is justified that the former was probably antecedent to the latter. In other words, the time sequence conforms with the morphological gradations represented by these fossil hominids. Of course, this general statement must not be taken to imply that the local varieties of *Australopithecus* found in South Africa were *themselves* the ancestral stock, for the genus may have had a much wider geographical distribution, and it may be that the South African types were local variants which persisted there for some time after other populations of the same genus in another part of the world had already given rise to the more advanced hominids of the *Pithecanthropus* stage of evolution.

An important aspect of *Australopithecus* is the great variability shown by different individuals and local groups, even in the circumscribed regions of South Africa in which their remains have been found. Again, as in the case of *Pithecanthropus*, there has been a tendency to interpret this variability in terms of different genera and species, and it seems to me that this has introduced the same sort of unnecessary complication into the picture. It may be emphasized again that it is the genetic fluctuation within populations that provides the basis for the selective action of the environment, and herein lies the real importance of the range of variation within the genus *Australopithecus*. As a matter of fact, some of the australopithecine specimens, at any rate as far as the jaws and teeth are concerned, approach very closely indeed to *Pithecanthropus*, so that a transition from one to the other can readily be envisaged without the need to "fill in" large gaps by hypothetical connecting links.[4]

[2] Some of the apparent differences may be related to individual or local group variations. For example, in two of the pelvic specimens the ischial tuberosity appears to be unusually small (though accurate measurement is rendered difficult by local erosion). But in one immature specimen from Makapan, in which the tuberosity is excellently preserved, it is closely comparable in width to that of an immature Bushman pelvis.

[3] It is important to note, when making reference to publications which are not entirely recent, that the main subdivisions of the Pleistocene have lately undergone revision. Thus, much of what used to be called Lower Pleistocene is now Middle Pleistocene, and what was once regarded as the terminal phase of the Pliocene is now taken to be Lower Pleistocene.

[4] The few specimens of australopithecine jaws here referred to were allocated by their discoverers to a separate genus, *Telanthropus*. But there appears to be no really convincing evidence that the differences which they show from other specimens of *Australopithecus* exceed, either in degree or kind, the variational limits known to exist within the single genus *Homo*.

The hominid status of *Australopithecus* has been conclusively demonstrated by extensive anatomical studies, and quite recent discoveries have now given rise to the suggestion that, in spite of the small size of the brain, the South African representatives of this genus may even have been sufficiently advanced culturally to have been capable of fashioning crude stone implements. At any rate, definite artifacts have been found embedded in breccia which also contained remains of *Australopithecus,* but which has not been found to contain any remains of a more advanced type of hominid. Clearly, this is a most exciting discovery, but perhaps not altogether unexpected. For attention had previously been drawn to quantities of baboon skulls associated with australopithecine remains, most of which show depressed fractures of the roof of the skull which suggest the possibility that they had been killed by skilful blows with an implement of some sort. The obvious inference from the discovery of the stone artifacts is that they were actually fabricated by the australopithecine individuals whose remains were found close alongside them. But there still remains the possibility that there *was* a more advanced type of hominid occupying the same region which may have been the actual tool maker, even though it has to be admitted that so far no remains of this problematical type have come to light. If, as the result of further search, it should be established that similar crude artifacts are to be found at several independent sites in association with australopithecine remains (but with no remains of any more advanced type), this would no doubt be acceptable as sufficiently good evidence of the tool-making capacity of *Australopithecus.* Naturally, the question has also been raised whether a creature with so small a brain could have possessed the intelligence required for tool-making. But this is a question which cannot at present be answered with any assurance. Taking into account the extraordinarily wide range of variation in the cranial capacity of modern man—from less than 900 cc. to about 2,300 cc. in people of apparently "normal" intelligence—and taking into account also the fact that no marked correlation has been discovered between intellectual ability and cranial capacity in normal people, it seems that within very wide limits the absolute size of the brain gives no indication of degrees of intelligence. It has to be remembered, further, that while the cranial capacity of fossil hominids can give information on the brain volume, it provides no information of the complexity of organization of the nervous tissue of which it was composed.

We have now traced in retrospect a graded morphological series, arranged in an ordered time sequence, linking *Homo sapiens* through Early Mousterian man, pre-Mousterian man, and the small-brained *Pithecanthropus,* with the still smaller-brained *Australopithecus.* This sequence comprises a remarkable confirmation of the connecting links postulated and predicted by Darwin's hypothesis of the descent of man, at any rate as far back as the Early Pleistocene. There is no conspicuous gap in the sequence, but there still remains a serious gap covering the preceding period of the Pliocene. We know that during the early part of the Pliocene, and throughout the Miocene period before then, many interesting varieties of anthropoid apes were distributed over wide areas of the Old World, in Europe, Asia, and Africa. It is also the case that some of these fossil apes show generalized features of the skull, dentition and limb bones which might well have provided the structural basis for the subsequent emergence and differentiation of the hominid line of evolution. But as yet we have no objective evidence to show just when, or how, the emergence of this new line took place.[5]

Darwin in his time found it necessary to emphasize the imperfection of the geological record to account for the absence of many of the connecting links demanded by his conception of the evolutionary process. Since then, of course, the continual accession of fossil remains of all kinds has amplified the record enormously, and has provided much of the crucial evidence for the succession of intermediate types. But so far as human evolution is concerned, we in our time still find it necessary to emphasize its imperfection, and to re-emphasize Darwin's words, "The crust of the earth with its embedded remains must not be looked at as a well-filled museum, but as a poor collection made at hazard and at rare intervals." It is an unhappy circumstance that during the Pliocene period (which lasted about ten million years), and during the succeeding Pleistocene,

[5] Reference should be made to a fossil Primate, *Oreopithecus,* whose remains have been recovered from Early Pliocene deposits in Italy. Mainly on the basis of dental characters, this type is regarded by some good authorities as an exceedingly primitive representative of the Hominidae. But there are certain anomalous features of the dentition, as well as the paucity of material so far available, which appear to me to render such a conclusion rather doubtful for the present.

climatic changes and earth movements were accompanied by erosion and denudation of the earth's surface on a vast scale; as a result, geological deposits which may have contained valuable relics of the earlier connecting links of hominid evolution have been completely destroyed and removed. At any rate, fossiliferous Pliocene deposits in those parts of the world, such as Africa, where such connecting links may be presumed to have existed are rarely found—particularly deposits of the Upper Pliocene which was probably the critical period for tracing the course of hominid evolution which was immediately antecedent to the *Australopithecus* stage.

In view of the hazards which must always attend the preservation of fossilized remains, even under the most favorable circumstances, it is not a little remarkable that our record of the later phases of hominid evolution is as good as it is. A sequence of fossils in any other mammalian group equivalent in their close gradation to the sequence *Australopithecus* → *Pithecanthropus* → *Homo* would be regarded by most vertebrate palaeontologists as a highly satisfactory record. For even if it should prove not to represent a linear sequence of evolution (which it most probably does), it at least provides the concrete and objective evidence of a general evolutionary trend. It is an interesting fact that each discovery of a possible connecting link in human ancestry seems always to arouse more contentious and more prolonged disputation than equivalent discoveries relating to the ancestry of other mammalian species. Indeed, considered in retrospect, some of these argumentations may appear to us to savor of the ridiculous and comical, if only for the reason that such unlikely interpretations seem often to have been based on evidence the real purport of which we now accept as reasonably well assured. But, as I have already noted, the peculiarly personal nature of the study of our own origin necessarily introduces an emotional bias which tends to affect our judgment of the evidence, and this fact needs constantly to be kept in mind. Probably one of the main causes of misunderstanding in the study of hominid evolution is the use and misuse of the colloquial terms "man" and "human." Not even anthropologists always employ these terms consistently, but the main difficulty is that they are terms which in ordinary usage are commonly taken to imply very much more than the meaning attached to them by biologists when they are considering man in a strictly biological sense. It is for this reason that I would like to insist that, in discussing the evolutionary origin of our own species, the biologist should avoid altogether the terms "man" and "human"—except only where there can be no possible misunderstanding about what he means by them. Undoubtedly, also, we can approach this whole problem with much greater objectivity if we confine ourselves (even at the risk of being accused of pedantry) to the scientific terms of zoology, such as *Homo* (meaning the generic group of which *Homo sapiens* is one of the species—in fact the only surviving species), and the Hominidae (an inclusive term meaning the zoological family of which *Homo* is one of the genera).

Darwin wrote: "In a series of forms graduating insensibly from some ape-like creature to man as he now exists it would be impossible to fix on any definite point when the term 'man' ought to be used." The discovery since the publication of *The Descent of Man* of fossil types comprising mosaics of "ape-like" and "man-like" characters—in fact of just those types the former existence of which Darwin had "predicted" from the less direct evidence then available to him—now makes it clear that confusion and misunderstanding in any future discussions on hominid evolution can only be avoided if the strictest attention is paid to the customary rules of scientific nomenclature.

The very fact that it has now become necessary to emphasize this need for the most careful attention to nomenclature is surely an impressive testimony to the essential accuracy of the thesis expressed by Darwin that "man is descended from some lower form."

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THE CONCEPT OF NATURAL SELECTION: A CENTENNIAL VIEW

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SEVERAL years ago, Sir Isaiah Berlin in writing an essay on Tolstoy's philosophy of history took his text from a fragment of the Greek poet Archilochus, which said: "The fox knows many things, but the hedgehog knows one big thing." Berlin's imaginative interpretation of this line was that writers, thinkers, or perhaps, all of humanity, can be divided into the two classes of foxes and hedgehogs. The ideas of the foxes are centrifugal, diffuse; they range over a variety of levels not integrated by a single theme; they lack a unifying focal point. In the realm of thought and creation the foxes follow many ends which may be unrelated and which do not form a cohesive system. The hedgehogs, on the other hand, are characterized by centripetal thinking directed towards a unitary inner vision. They are single-minded in their intellectual pursuits and, no matter how versatile they may be in their endeavors, the hedgehogs point to and are guided by the one big thing. Aristotle, Shakespeare, Balzac were foxes. Plato, Dante, Dostoyevsky were hedgehogs. Had Berlin considered biologists, he might well have placed Pasteur among the foxes. Darwin would most certainly have stood supreme as a hedgehog.

The one big thing towards which Darwin's thoughts and writings were directed was, perhaps, not so much Evolution as the principle of Natural Selection. This was the concept that allowed the formulation of an acceptable theory of secular change in organic nature. Evolution had been discussed for more than two millennia before Darwin and Wallace. The idea, however, lacked conviction because, in the face of so much evidence for it, no generally comprehensible way in which evolution could have occurred was apparent to its proponents. Even the notion of natural selection was not exactly brand new in 1858. As an explanation of the presence of adaptations within species it had been considered by one or another natural philosopher from classical antiquity onwards. But as a mechanism for the origin of species, natural selection was apparently advanced only in the nineteenth century. The South Carolina-born Dr. Wells mentioned it as if he took it for granted in "An account of a white female, part of whose skin resembles that of a Negro" some forty years before Darwin and Wallace. Patrick Matthew apparently alluded even more casually to natural selection a few years later in an appendix to a volume on *Naval Timber and Arboriculture*. Yet the revelation that a single principle can embrace the evolutionary changes in all systematic categories, that the same basic process is operative at all levels of life wherever self-replicating units exist, came from Darwin and Wallace.

Their one big thing, natural selection, set at rest the doctrine of special creation. In combination with our knowledge of Mendelian inheritance acquired since Darwin's day, it rendered obsolete such alternative theories of evolution as were based on extra-mechanical agencies, or on direct adaptation of organisms to their immediate environment (that is, on inheritance of acquired characters), and exposed them as sins against Occam's razor. Natural selection furnished the binding principle for a general or unified theory of historical change in the living world. It made evolution not only understandable and acceptable but, beyond that, caused it to become of commanding significance in man's thinking about himself.

OBJECTIONS TO NATURAL SELECTION

This is not to say that the doctrine of natural selection was generally accorded, immediately upon its appearance, the status of dogma. In fact, over the last hundred years the thesis of natural selection has been doubted, questioned, derided, ridi-

culed, and on several occasions buried with considerable pride, pomp, and circumstance. Nevertheless, over the passage of years the concept has weathered its criticisms and survived its funerals, gathering strength after each successive interment. No serious student of biology today questions the actuality of organic evolution. Neither is there any disagreement as to the reality of natural selection, although its importance relative to other phenomena responsible for descent with modification may be in dispute. Even those considered to be militant foes of the view that natural selection is of primary significance in all phases of the evolutionary process, acknowledge, as for example did the late Richard Goldschmidt, that "every biologist agrees that selection and isolation are the basic working methods of evolution." The objection that Goldschmidt took towards what he used to call hyper-selectionists was not addressed to their belief in selection but rather to their ideas as to what was being selected. Thus arguments may still flourish as to whether selection operates with respect to minor or major mutational steps, how exclusive an agent it is under one or another circumstance, in what particular way it interacts with other processes in determining a given evolutionary change, whether it has been completely suspended in man under the recent developments in combatting sterility, disease, and old age, and with respect to many other issues. But there is no longer any doubt that natural selection is more than a theoretical possibility—it is unquestionably a logically imperative necessity in any accounting for evolution.

Generally speaking, there have been six kinds of criticisms raised against natural selection. The gravamen of the first kind was against evolution itself rather than natural selection as such. This issue is of no significance today. Secondly, teleologically minded biologists objected to the apparent purposelessness of natural selection. Condemnation on these grounds has little validity in the climate of present-day science, though I shall have occasion to return to this point in another connection. Thirdly, Darwin's own hypothesis regarding the basis of hereditary transmission created difficulties for the concept of natural selection. They were, however, dispelled when Mendelism entered the scene. Fourthly, Mendelian inheritance itself was misguidedly used to buttress the opposition to natural selection. Population geneticists have effectively demolished criticisms of this type; moreover they have demonstrated how particulate inheritance following Mendelian principles greatly augments the probable role of natural selection in evolution. Fifthly, objections have been raised, undoubtedly justifiably, against the intemperate support of natural selection by its earlier proponents, who attributed to the process consequences which we now know are ascribable to mating system, isolation, chance, and interactions of these factors with each other and with selection. And lastly, the most common and continually recurring opposition to natural selection is based on a misunderstanding of what is meant by the term. In spite of the fact that in recent years Fisher, Wright, Haldane, Muller, Dobzhansky, Ford, Simpson, Mayr, Stebbins, and countless others have repeatedly expounded the concept of natural selection, it still seems to remain an uncrossable *pons asinorum* for many refractory naturalists. It is difficult to know what, if anything more, should be done about this class of objections.

None of these categories of dissent from the idea of natural selection is a matter of serious concern at the present. Proof of the participation of natural selection in some situations is, of course, not tantamount to proof of its sufficiency to account for all evolutionary change. But no serious student of the subject insists on this extreme view. It is enough to say that the notion of natural selection as a major component of the evolutionary process has not only been theoretically established and empirically observed in the wild and in the laboratory, but it no longer falls entirely within the qualitative realm of science: natural selection can now be quantitatively treated and in many instances has been actually measured.

Thanks to post-Mendelian studies on the bases of hereditary transmission, and particularly to the developments in both theoretical and experimental population genetics in the last thirty years, our understanding of the operation of selection in nature has been vastly increased. Because of that, a prodigious embarrassment of riches on which to base a general discussion faces any reviewer of the subject. I shall therefore confine myself to a few aspects of the issue at large, trusting that other contributions to this program will cover at least some of the territory I neglect. In particular, I propose to pass over the speciation or splitting level of evolution, since it involves interaction with isolation, which is to be considered here by others infinitely more versed than I in this question. I should also note that, in con-

sidering post-Darwinian advances in the field of natural selection, I prefer omitting all mention of individual contributions to the risk of finding myself sire to an invidious, or even a merely provocative, list of names.

THE DEFINITION OF NATURAL SELECTION

It may be appropriate at this point to define natural selection. Darwin himself did so in a number of ways. Thus (quoting from the sixth edition of *The Origin of Species*), he says:

> As many more individuals of each species are born than can possibly survive; and as, consequently, there is a frequently recurring struggle for existence, it follows that any being, if it vary however slightly in any manner profitable to itself, under the complex and sometimes varying conditions of life, will have a better chance of surviving, and thus be *naturally selected*. From the strong principle of inheritance, any selected variety will tend to propagate its new and modified form.

Elsewhere we read:

> This preservation of favourable individual differences and variations, and the destruction of those which are injurious, I have called Natural Selection, or the Survival of the Fittest.

Some exegesis of the operative words in these passages is called for. In particular, three questions may be asked. Is Darwin's term *selection* synonymous with *choice?* Is *survival* to be taken in the precise meaning of the word or is it used figuratively, including the ability to reproduce? What does the term *fittest*, which Darwin adopted from Herbert Spencer, signify in the context of the rest of the definition?

Regarding the first question, Darwin says:

> In the literal sense of the word, no doubt, natural selection is a false term, but who ever objected to chemists speaking of the elective affinities of the various elements?—and yet acid cannot strictly be said to elect the base with which it in preference combines. It has been said that I speak of natural selection as an active power of Deity; but who objects to an author speaking of the attraction of gravity as ruling the movements of the planets? Everyone knows what is meant and is implied by such metaphorical expressions; and they are almost necessary for brevity. So again it is difficult to avoid personifying the word Nature; but I mean by Nature, only the aggregate action and product of many natural laws, and by laws the sequence of events as ascertained by us.

It seems clear that, despite the fact that Darwin in his argument leaned very heavily on analogies between the results of purposeful and directed artificial selection of plants and animals by man with what is observed in the wild, he did not see in selection a process in which deliberative judgment or choice on the part of any agency plays a part.

With respect to the second question, the meaning of survival, the vast majority of writers on evolution take Darwin's usage of this word literally. They assume that Darwin meant that discrimination between what he considered the fit and the unfit was entirely by death and did not involve the broader and more relevant differences in ability to produce living offspring. Darwin, however, was not as naive as he is often represented. In discussing struggle for existence, he says: "I should premise that I use this term in a large and metaphorical sense including dependence of one being on another, and including (which is more important) not only the life of the individual, but success in leaving progeny." Thus, although Darwin may have erroneously accepted the view that survival is necessarily the major component of natural selection, he understood that the crux of the selection process lies not merely in the ability of an individual to survive longer than others, but in its greater capacity for production of living offspring; that is to say, not only in survival of individuals within a generation, but of groups over a period of generations.

This fact enables us to answer the third question, that regarding the interpretation which must be given the word *fittest*, or rather, the term *fitness*. The expressiveness of Spencer's superlative seduced Darwin into accepting "survival of the fittest" as being equivalent to "natural selection." As a result, many early evolutionists and a fair proportion of those naturalists of today whom the literature of population genetics has bypassed attached anthropomorphic value judgments to selection. Yet neither strength of character nor moral goodness, neither extreme size nor high intelligence, nor even long life *per se* causes an individual to produce more offspring, that is to say, make it fit in Darwin's sense. Indeed, often organisms which are totally undistinguished by any physical standards, organisms exhibiting average dimensions for various properties, in fine, individuals which are mediocre for any traits obvious to the human eye, are the ones that are most successful in propagating themselves. They are therefore the *fittest*. If there is

one thing upon which the most factious partisans of various currents of evolutionary thought agree, it is that fitness of an individual, in the context of the natural selection principle, can mean only the extent to which the organism is represented by descendants in succeeding generations. Fitness can be discussed in absolute terms or expressed relatively to the average of a group. Immediate or more remote generations of descent may be chosen as a point of reference. Enumeration of offspring or some other way of assessing the "amount" of progeny left may be resorted to. But in all instances, fitness must refer to the ability of an organism to leave surviving offspring.

A habitual fallacy, shared by both the opponents and the supporters of evolution by natural selection, is the idea that any part of evolution may be explained by saying that the fittest individuals have the most offspring. When fitness is considered with reference to evolutionary phenomena, such statement is logically circular and begs the question. If capacity of reproduction is the criterion of fitness, the only connecting proposition between reproduction and fitness which avoids tautology is that individuals having most offspring are the fittest ones. This is neither an assumption, nor a hypothesis to be proven, but merely a definition.

Darwin's description of natural selection can now be paraphrased to say (1) that in nature individuals differ among themselves, (2) that their differences are in part determined by heredity, and (3) that, therefore, whenever these differences are correlated with fitness, that is, success in leaving offspring, the properties of the more fit individuals will be represented in succeeding generations to an increasing extent. Thus, changes in the make-up of successive generations are determined in a measure by the inequalities between the reproductive rates of individuals differing in hereditary endowment, that is to say, by different *genotypes*. More concisely, natural selection then is the *differential reproduction of genotypes*. The carriers of various genetic constitutions have *phenotypes* (to wit, somatic properties whether or not they happen to be apparent to the human observer) which differ in their capacity to produce surviving progeny in their particular environment. The genotypic composition of the next generation is then modified, and changes in phenotypes are produced to the degree to which phenotypes are genetically determined.

ADVANCES SINCE DARWIN

Darwin and Wallace arrived at their conclusions about the role of natural selection in evolution by deduction. Assuming the validity of their basic premises, natural selection can be inferred as a consequence independently of actual experience. *The Origin of Species* was essentially an attempt at *a posteriori* justification of Darwin's thesis based on the mustering of a great volume of descriptive evidence in its support. Since 1859 the premises underlying Darwin's chain of reasoning have been subjected to test many times. Thus, differential reproduction of individuals could often be ascertained by counting and statistical analysis of only a moderate degree of sophistication. Similarly, the dependence of such differential reproduction at least in part on hereditary differences was demonstrated both by verifiable inference from observation in nature and by laboratory experiment. But our achievements since Darwin are not limited merely to a further accumulation of examples (including those in ultramicroscopic organisms not even dreamt of in Darwin's philosophy) or to the development of less equivocal proofs of evolution than Darwin had at his disposal. Much more can be said about post-Darwinian advances in the study of natural selection. A sampling of illustrations chosen from different areas of evolutionary knowledge charted in recent decades bespeaks this fact.

The first of these may be provided by the insight that has been acquired into the basis of hereditary transmission. It is this knowledge that furnished the necessary link between selection and evolution. Darwin made somewhat vague references in *The Origin of Species* to the operation of the "strong principle of inheritance." He was fully aware of the deficiencies in his knowledge of the mechanism of heredity. They led him to formulate a speculative and somewhat improbable, even in the light of a century ago, hypothesis of blending inheritance. This principle in turn forced Darwin to espouse the postulate that acquired characters were transmissable, because otherwise continued variability in natural populations could not be accounted for. It was not until Mendelian theory was developed that such pathetically artless conjectures as, for instance, the direct hereditary effects of use and disuse of organs and parts of the body, became superfluous. Three aspects of Mendelism were especially important in this connection: (1) the particulate basis of the units of inheritance to which we may refer as *genes*, (2)

the distinction between phenotype and genotype, and (3) the statistical nature of the phenomena of heredity. It was also in large part Mendelian inheritance that resolved the problem of persistent variation and, more generally, led to the possibility of quantifying evolutionary processes.

Symbolic representation of evolution, taking into account all but unique events, has now been arrived at. It is based on the description of the evolutionary process in terms of changes in the frequencies of alternative genes (or chromosomes) in a population. Indeed, the expression "survival of the fittest" can be applied with much more justice to the behavior of genes over many generations than to that of individual organisms within one. From the quantitative approach an understanding of the components of selection-induced alterations in fitness (those due not only to changes in gene frequencies, but also to modifications of the environment and of the mating system, as well as to gene interaction) has been gained. Methods for estimating the extent to which a population can be transformed by selection have been devised. Quantitative bases for systems of correlated response (i.e., effects on traits which themselves are not being subjected to selection pressure) characterizing changes under selection have been established. The utility of these developments for breeding practice is obvious. But equally important are the possibilities they have opened for a quantitative approach to selection in terms of observations of living beings in nature or of the paleontological record.

Another sphere of study which has contributed to an increased comprehension of a natural selection is that dealing with the materials on which selection operates. The notion that individuals differ in hereditary endowment presupposes that a mechanism by which such differences can arise exists. Selection experiments, followed by the discovery of artificial means of producing mutations in the hereditary material, and the many elaborate investigations on the nature of mutational changes and effects, made it clear that hereditary variants on the gene level do not arise as a consequence of selection. Variability for selection to act upon must therefore be supplied by mutation (or subsequent to mutation, by hybridization). It is not entirely correct to say, as has often been done, that the mutation process is a completely haphazard one. The structures that mutated genes can assume are not random. For instance, not all possible combinations of the elements of which genes are made possess the power of self-duplication, without which genes would not exist. But the non-randomness of mutations does not mean that selection determines the direction of phenotypic effect which gene mutations have.

More recent studies, including those on the physical chemistry of hereditary material, may be expected to clarify eventually many related points which are still obscure. For example, the question of how random the genes subjected to selection are with respect to their spatial relations within organized units of higher order, such as chromosomes, needs additional elucidation which breeding experiments with any of the higher organisms are incapable of supplying efficiently. Similarly, the relation between the amount of actual structural change involved in a gene mutation and the degree of phenotypic effect the change may lead to in the developing or adult organism still remains to be explored. The relative importance in different circumstances of the hierarchy of selection materials—genes, chromosomes, genomes, total genotypes, populations—is another aspect of evolution on which more light may be expected to be forthcoming.

On another level, the relationships between natural selection and adaptation has been illuminated by the semantic analysis of the term fitness. The early evolutionists chose their examples of adaptive traits, presumed to have originated by selection, on the basis of entirely anthropomorphic interpretations as to what constitutes an advantage to a plant or animal. We now know that adaptive traits are those contributing to increased fitness in any way whatever, rather than only those with spectacular manifestations on the ingenuous level of Kipling's *Just So Stories*. The important effects of natural selection are more subtle than the provision of tigers with stripes or leopards with spots for alleged purposes of camouflage. Physiological and biochemical properties very often are more likely to be of significance in determining an individual's fitness than are conspicuous morphological differences which sometimes may be by-products rather than criteria of selection. Moreover, fitness is determined by a combination of a great many somatic features, or rather by the phenotype as a whole. It follows from this: (1) that the selective value of any one character may vary, depending on the particular totality of traits in which it is found, (2) that the selection pressure applied to any single trait (which, of course, is an abstraction by an investigator from the total

phenotype) is bound to be very small, and (3) that, considered with respect to single genes, the process of natural selection is usually very slow. These deductions accord well with the evidence on the rate and complexity of evolutionary change in nature which tended to puzzle the early Darwinians.

They also lead to the idea that the most adapted kind of individual is not one conforming to some phenotypic norm, but rather one whose development and reproductive life history is adjustable to varying environmental conditions in such a manner as to preserve high fitness. The most successful population is similarly one that can meet the challenge of environmental changes between generations. In other words, homeostatic devices stabilizing the individual's own reproductive performance have a high selective value, while a heterogeneous genetic make-up, even behind a uniform phenotypic façade within a single generation, may be an advantage to a population. These considerations, backed by ever-accumulating experimental and descriptive evidence, suggest the importance in evolutionary thought of such concepts as buffered and balanced genotypes, integrated gene pools, and coadaptation, which no doubt will be discussed on this occasion by others.

I would, nevertheless, like to call attention to these general ideas, without entering into the exposition of their full meaning, in alluding to some other aspects of natural selection. For one thing, they are of significance in the process in which natural selection, by utilizing interactions between components of genotypes, endows whole populations with properties transcending those attributable to their individual members. For another, these concepts are relevant to the currently controversial issue regarding the autonomy of single genes in the selection process.

Reducing the argument to its simplest terms, there is, on the one hand, the belief that the selective values of genes are reasonably independent of the genotypic combinations in which they occur. That is to say, genes which are found to be highly deleterious to fitness when forming part of one genotype are, in this view, considered extremely unlikely to be advantageous in another genotype. Ranged on the opposing side is the opinion that, since selection is primarily concerned with genotypes, the effects of individual genes in a given genetic context are not necessarily predictable from their behavior in another genetic background, be it only different with respect to a single member of a gene pair. Needless to say, the proponents of neither view claim that their interpretation entirely excludes the contrary one. Rather, the argument relates to the comparative importance of the two kinds of genes (those with predictable and those with unpredictable behavior) in evolution and in breeding practice. The same question can also be raised, with some poignancy, with reference to the human species, since, for example, estimates of the extent of genetic damage produced by ionizing radiation differ on the alternative hypotheses of gene action.

These broad issues also bear upon the relative importance of the different types of selection which we have learned to distinguish since Darwin's day. Thus *directional* selection produces transformation of a population along the time axis, while *disruptive* selection may result in the splitting of a group into subgroups. These two kinds of selection are progressive, in the limited sense of leading to new forms of life. *Stabilizing* selection is conservative. It operates by rejection of variants and maintains the population at an equilibrium. Of the several forms of pressure antagonistic to the preservation of fitness which selection must counterbalance, those of mutation and segregation are of greatest import. Elimination of deleterious mutants by selection is a process that has been long recognized. The significance of selection against non-optimal genotypes which arise in every generation as a result of segregation of chromosomes in the process of germ-cell formation, however, has been appreciated only recently. Studies from many fields, for example, those on wild and cage populations of *Drosophila*, on artificial irradiation, on the use of hybrid vigor in breeding economic plants and animals, on cytogenetics of grasshoppers, on aberrant forms appearing under intense inbreeding, and many others, argue for at least as great an evolutionary importance of selection against segregation as of that against mutation. Mutations are needed to provide a basis for further evolution. But the ones not useful at any given time in the phylogeny of a population are eliminated or kept from increasing in frequency by selection. Without selection against segregation genetic variability already present could be lost. William Blake's affirmation that "to be an error and to be cast out is a part of God's design" seems to be an apt description of selection against both mutation and segregation,

though invoking Blake in this connection leaves me open to the charge of citing the Scriptures to my own purpose.

Another evolutionary precept which has been recognized since Darwin (in fact, in contradiction to Darwin) is that selection, far from being blind, operating entirely by chance, and begetting successful kinds of organisms only as a result of improbable accidents, may be correctly described as a *creative* process. This term can, of course, be used in a variety of senses. In reference to natural selection its meaning is well illustrated by quoting what Michelangelo conceived the process of creation to be. The opening lines of one of his best known sonnets says in a somewhat free translation:

> The best of artists has that thought alone
> Which is contained within the marble shell;
> The sculptor's hand can only break the spell
> To free the figures slumbering in the stone.

In the same way, natural selection does not originate its own building blocks in the form of mutations of genes. But from them it does create complexes; it solves in a diversity of ways the great variety of problems that successful individuals and populations face; it builds step by step, even if by trial and error, entities of infinite complexity, ingenuity, and be one inclined to say so, beauty. Granted that it needs appropriate raw materials, that it may not necessarily be able to make a silk purse out of a sow's ear; yet, interacting with other evolutionary mechanisms, it has created the human species out of stuff which in its primordial stage may have looked no more promising.

MISCELLANEOUS IMPLICATIONS

The epithet creative is often interpreted to mean *effectively* causing, in the Aristotelean sense. Indeed, taking mutant genes and higher order components of genotypes as the *material* cause of evolutionary change, application of the adjective creative to natural selection is undoubtedly sanctioned by our present knowledge of the process. Nonetheless, the term raises some fundamental questions regarding causalities in evolution and may even provoke charges of teleology, long a dirty word in science. I do not mean, of course, that any mystical doctrines of ends involving inner perfecting principles or entelechy can be imputed to modern evolutionists. Neither design by supernatural agencies, nor an *élan vital*, from a comprehensive laboratory analysis of which we are supposedly forever barred, nor yet any guiding plan of morphological and physiological perfection, needs detain us in this discussion. Indeed, Bergson and other militant teleologists of yesteryear would find little comfort in the distinct possibility that, if there is an Aristotelean final cause of evolution which directed all preceding events in the animate world, it may turn out to be the Götterdammerung initiated by man's mastery of subatomic forces. Be that as it may, there is no necessity to assume that increased adaptation of organisms under natural selection represents the purposive end of the evolutionary process. Adaptation and adaptability simply provide means toward increased fitness; they should be viewed not as causes but as consequences of natural selection.

At the same time it must be realized that natural selection depends, in addition to variation (production of materials for selection to work on) and heredity (perpetuation of successful variants), on still a third factor, namely, the *potentiality* to produce young in excess of parental numbers. Only in the presence of this factor can inequalities of rate of reproduction between individuals exist in a group not heading for extinction. When the inequalities systematically relate to genotypic differences between individuals, natural selection is said to take place. In other words, while capacity for propagation beyond that needed to maintain constant population size does not ensure that natural selection will occur, it is a necessary condition for natural selection in any group which is to survive.

Darwin, who was, of course, mechanistically minded, spoke somewhat obscurely of the laws of Growth and Reproduction underlying selection. Samuel Butler came out directly with the vitalistic tenet that there exists a "universal innate desire on the part of every organism to live beyond its income." We may instead talk of an empirically discovered biological analogy to the first law of motion, namely that living matter if left alone will tend to increase itself indefinitely. Whatever the formulation, natural selection must always operate to maintain or to increase the frequency of genotypes which have the highest relative fitness. This process as a rule cannot lead to a decrease in absolute fitness except under special circumstances involving changes in the direction of selection or in mating system. The exceptions do not invalidate the proposition that natural selec-

tion *defined* as inequality of reproductive ability, that is to say, of fitness, also *causes* fitness to increase. Thus we are either attributing immanency to natural selection, or at the least, after having eliminated one tautology by our definition of fitness, we have come upon another. Logical dilemmas of this sort are, of course, not unique to the issues involved in natural selection or, indeed, to biology in general. I am sure that any competent philosopher could easily solve seeming paradoxes of this kind. The difficulty is that no two schools of philosophy seem to agree on the correct solution. It was for good reason that Bertrand Russell once said that causality is one of the two great scandals (induction being the other) in the philosophy of science. I have mentioned the problem here merely to indicate that, with all of the knowledge now acquired on the process of selection in nature, its logical status in evolution is still uncertain and undoubtedly controversial.

It was very likely misplaced confidence in their comprehension of natural selection or, perhaps, confusion between evolution as a law and natural selection as its instrumentality, that has led numerous social scientists and political philosophers of various hues and persuasions to project the notion of natural selection from biological to cultural systems. Such terms as progressive adaptation, struggle for existence, survival of the fittest, proved to be equally irresistible to materialists and idealists, to mechanists and teleologists, to prophets of *laissez faire* capitalism and to heralds of the proletarian revolution. Yet, as has already been noted, the only value connotation that natural selection in its proper interpretation has refers to reproductive ability. Furthermore, it operates in a self-perpetuating system of particulate units, the relative proportions of which in a population change as a consequence of selection. Is there really an exact or even a moderate analogy of this principle in social evolution?

If so, it does not seem to have been established by any of the varieties of self-styled social Darwinists, especially when social institutions are dealt with. It is, indeed, possible that intergroup selection occurs between religious or cultural segments of the human species whenever they differ in birth rates. But the often-asserted inevitability of communist domination of the world, for example, is not rooted in unequal reproductive rates. Again, ethically dubious business practices allegedly sanctioned by the purported natural law of dog-eat-dog, seem remote from the biological phenomenon from which they are supposed to derive support. Perhaps, the source of confusion does lie in the value constructs of "steady advance," "struggle for survival" and so forth, which have become attached to natural selection by its early enthusiasts. Darwin himself, taking the cue from Wallace, Galton, and Spencer, has unfortunately contributed to these mists of error, especially in *The Descent of Man*, though even in that book he confined himself, broadly speaking, to biological and not to social aspects of "natural selection as affecting civilized nations."

That organic evolution is based on natural selection can be considered to be demonstrated. Whether cultural evolution, in which generations communicate with each other by means different from information coded within replicates of the units of hereditary transmission, also is, remains to be seen. Needless to say, Mendelism is not a prerequisite to natural selection. Cytoplasmic transmission of particles, whatever its role in evolution is, can, no doubt, be shown to be subject to the same process. But self-propagation is essential to natural selection, whereas systematic historical changes in the extra-biological aspects of the world surrounding us could have happened without natural selection in the biological sense of the term.

A possible exception to this dictum may be found in the events leading to the origin of life. If autocatalytic processes of reproduction can be said to have occurred before protoplasm made its appearance on earth, chemical evolution culminating in living matter could have depended, as has been suggested by some, on natural selection. On the other hand, if the view is taken that self-reproduction is the exclusive property of living matter, natural selection cannot have antedated life.

One more point with reference to common misinterpretations of the basis of natural selection may be considered. It has often been said that the development of modern medicine and other technological advances combined with certain humanitarian and religious notions has led to the suspension of natural selection in man. As evidence, exercise of therapeutic measures against various congenital diseases is cited and examples are given from an increasing list of defects which used to be, but no longer are, disabling. It is assumed that carriers of genotypes predisposing to such conditions were in the past at a selective disadvantage, while currently their reproductive ability is not under any handicap. Hence, it is

argued, natural selection is being interfered with by euthenic measures. More often than not, a dire warning that the human race is thereby slowly committing suicide is added.

It is entirely true that many genotypes which rendered their possessors unfit in earlier days do so no more. Natural selection now, therefore, is not based on the same components of fitness or results in the same directional changes as before. But this is by no means the same thing as saying that natural selection is not operative. What has happened is that the environment, the adjudicator of which genotypes are fit, has been altered. The therapy that has become available is a feature of the new environment. The determinants of fitness may have become changed, but inequalities in reproduction were not thereby eliminated. An analogy is provided by one of the classical cases of empirically observed natural selection in a lower form of life.

In certain species of moths dark and light colored forms occur. The dark kind is generally hardier and hence would have been expected to be more fit. However, its melanic pigmentation makes it more conspicuous to predators. Therefore, in early observations at certain localities the light forms were generally found to be more numerous than the dark ones. Since the Industrial Revolution, however, increasing amounts of soot and similar waste products began to spread around the countryside. This provided increased protection to the melanic forms in manufacturing districts. As a result, their higher reproductive capacity now gave them an advantage over the light forms so that in many industrial areas the latter now approach extinction. Natural selection here has reversed its direction. A gene that was deleterious in its net effects in the earlier environment has now become advantageous. The basis of fitness has been changed, but natural selection still went on. This kind of change has undoubtedly occurred many times in the past history of man, for instance, when fire-making tools were invented, thereby affording protection to some genotypes which were formerly disadvantageous.

Susceptibility to many diseases may then not contribute any more to differences in fitness of man. It is not impossible that resistance became in some instances an encumbrance. More likely, however, major importance in determining fitness was assumed by genes in control of other phenotypic traits. For instance, the genetically determined aspects of the ability to provide young with food obtained by strength may have now lost their positive selective value. On the other hand, genes for philoprogenitiveness in a world in which conception is under man's volitional control may have become of correspondingly greater import in the selective process.

Exactly how disgenic in terms of human values today's natural selection may be is difficult to tell. Selection which might have the most serious potential consequences to mankind could be that operating through the medium of differential reproductive rates of groups with differing intelligence. However, there are reasons to believe that this process may be of the stabilizing kind, maintaining constant genotypic frequencies rather than shifting them in a direction commonly agreed to be an undesirable one.

Generally speaking, selection in man is probably not as stringent as it was in the past, though this is by no means certain. The immense increase in the average number of surviving offspring which occurred in the last century does not of itself constitute conclusive evidence for lowered selection intensity. In any case, the actual reproductive rate in man is, of course, still greatly below its biological maximum, which means that there is still considerable opportunity for selection to occur. Evidence that inequalities in fitness currently observable are independent of genotypic constitutions would doubtlessly be difficult to obtain. Even so, it would seem that only when man has achieved such complete mastery over his environment that all possible human genotypes will be equally likely to produce the average number of surviving progeny, can we be sure that natural selection has ceased in our species.

IN CONCLUSION

I have ranged somewhat widely, even if not deeply, over the subject assigned to me. Before closing I would like to make it clear that population genetics, the discipline which has contributed most to our present understanding of natural selection, is only entering the stage of adolescence. Its attainment of maturity depends on a synthesis with its sibling doctrines of physiological, biochemical, and other branches of genetics, which should bring into fuller clarity our picture of evolution, and should fill the numerous gaps in our knowledge of the organic world. Evolution is the most fundamental biological law yet discovered. Natural selection is the basic mechanism implementing it. The principle of descent with

modification, creatively, albeit opportunistically, husbanded by natural selection, is as firmly established as any concept in biology. But what we have learned so far about natural selection is obviously only the beginning. What remains to be learned is immeasurably more. Truth, said Bacon, is the daughter of Time, and one hundred years is not a long period in the history of mankind. Furthermore, giant-slayers abound in the scientific woods through which we have to travel to our goal of understanding ourselves and the living universe. It is then not inconceivable that the role now assigned to natural selection some day may have to be reevaluated. However, if more adequate explanations are found for the phenomena in the animate world which we currently view as being consequent to natural selection, the ensuing revolution in our thought will have to be as great as that produced by Darwin and Wallace a century ago.

VARIATION AND HEREDITARY TRANSMISSION

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(*Commemoration of the Centennial of the Publication of* The Origin of Species *by Charles Darwin, Annual Meeting of the American Philosophical Society, April, 1959*)

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DARWIN'S WONDERS OF INHERITANCE

It is well known that Darwin regarded his book on *The Origin of Species* as an "Abstract."[1] In it he could give no more than the general conclusions at which he had arrived during the two decades of patiently accumulating and reflecting on all sorts of facts which could possibly have a bearing on his subject. But he was strongly aware of the necessity of later publishing in detail all the facts on which his conclusions had been grounded.

A large part of this duty was discharged by Darwin in 1868, in his two volumes on *The Variation of Animals and Plants under Domestication.*[2] It is in this work that Darwin comes nearest to the subject of genetics. Three long chapters are entitled "Inheritance" and many others deal with essential genetic problems. One is touched deeply when one reads these sections today and contemplates the difficulties which Darwin encountered and his persistent and ingenious attempts to overcome them. "The whole subject of inheritance is wonderful," he exclaims at the beginning of his account.[3] It is still a wonderful subject, but wonderful in a sense different from that in Darwin's mind. To him the whole subject then seemed unintelligible, full of wonders, even though he tried to interpret all his facts by a remarkable "provisional hypothesis" to which we shall turn later. Today many of the same facts can be understood by means of the insights of modern genetics, insights which have shifted the sense of wonder to a deeper plane.

It would be an instructive exercise to ask modern beginning students to read Darwin's chapters and to interpret the wonders Darwin enumerated in terms of what they just have learned. He deduced from his material that inheritance is the rule and non-inheritance the anomaly. But—to make use of many of his own words and phrases—he found this power of inheritance often to appear to us in our ignorance to act capriciously, transmitting a character with inexplicable strength or weakness. The same trait, as the weeping habit of trees or silky feathers in poultry seemed to be inherited firmly in some and not at all in other individuals of the same species. He notes that some characters have certainly been inherited from an extremely remote past and may therefore be considered as firmly fixed. But he also knows that under domestication some traits, after having been retained in nature for countless generations, have ceased to be transmitted in their original form. He cites cases where parents failed to transmit their likeness to the children who come to resemble a grandparent or a remote ancestor. He is aware that this is often due to the breed having been crossed at some former period. But he cites other examples where reversion to some ancient character has taken place without previous crossing. He is impressed by the fact that a father may transmit traits, invisible in his daughters but through them to his grandsons, and that mothers likewise may transmit features to their granddaughters through unaffected sons.

MENDEL, NAUDIN, AND DARWIN

All these and other facts collected by Darwin are still recognized as such but not one of them is now seen to be contradictory to another. A few generalizations due to Mendel and his followers were the keys to many of Darwin's riddles. Mendel showed that in most organisms the elements of the hereditary material, the genes, occur in pairs, one derived from each of the two parents;

[1] Darwin, Charles, *On the origin of species by means of natural selection*, 1, London, John Murray, 1859.

[2] Darwin, Charles, *The variation of animals and plants under domestication*, 2 v., London, John Murray, 1868.

[3] *Ibid.* **2**: 2.

that two individuals may appear alike even though one of them has two identical genes instrumental to the development of a given trait and the other only one such gene, its different partner remaining without any outward expression. This phenomenon of the action of a dominant gene covering up that of its recessive partner can account for the reappearance of a trait which had been absent for generations. The recessive gene may be transmitted unnoticed for generations by one of the parents, but its effect will become apparent when two carrier parents each endow their offspring with a recessive gene only and not with its dominant companion. The expansions and experimental verifications of this simple genetic scheme are well able to clarify some of the more complex phenomena which perplexed Darwin. Thus, the peculiar types of transmission of fully and partially sex-limited traits, mentioned above, are now understandable in terms of the transmission of ordinary genes whose expression is controlled by the sex of the individual in whom they reside, or of a class of genes which contrary to the main rule occurs as pairs in one sex only, but as solitary units in the other.

Darwin's own attempt at an interpretation of the facts of inheritance was based on postulating the existence of numerous genelike elements, called gemmules, which were thought to be present in all parts of the body, to multiply by self-division, to circulate freely in all parts of the organism, and to be collected in the sexual cells. The simultaneous presence of what we now call the dominant and the recessive member of a pair of genes, in Darwin's provisional hypothesis of pangenesis, was represented by the simultaneous presence of many gemmules of the kind which became expressed in the individual and of some of another kind which showed their presence only under special circumstances. The provisional character of the hypothesis involved sufficient numbers of degrees of freedom to make it adjustable to a large variety of observations.

It has often been asked whether Darwin would have recognized the solution, had he known of it, that Mendel had provided for the wonders of inheritance. Mendel's paper appeared in press in 1866,[4] two years before Darwin's *Variations*. It remained unknown to most biologists including—it seems clear—Darwin, who otherwise undoubtedly would have quoted from it. Darwin knew of Naudin, Mendel's French predecessor and referred to his work extensively and with high respect. He would have appreciated some of Mendel's findings on hybrids of garden peas and their interpretation but, would he have been willing to accept them as of general validity? Darwin and Naudin were convinced that more than one pollen grain is needed for successful fertilization of an ovule but Mendel's interpretation required the transmission of single elements from each parent. Darwin was impressed by the similarity between variations arising among sexually produced offspring and among forms derived from buds and other types of asexual tissues. There was no place for such bud variations in Mendel's early scheme of things. This latter topic still disturbed Bateson, the great protagonist of Mendelism, in the twenties of the present century.[5]

Published proof that fertilization of an egg by a single male germ cell is sufficient for development and that participation of more than one such cell is usually lethal did not come until ten and more years after Mendel's report—although Mendel himself, stimulated by his knowledge of Naudin's and Darwin's contrary opinions, made the crucial experiment in 1868. He told Nägeli in one of his private letters that from fertilization of the flowering plant *Mirabilis jalappa* with single pollen grains he obtained 18 well-developed seeds and from these an equal number of plants![6] Darwin, unaware of this experiment, which seemed so important to Mendel that, in spite of an eye ailment, he could not bring himself to postpone it to some later date, might well have deferred judgment on Mendel's genetic conclusions of 1866. And it should not be forgotten that Mendel himself was not convinced that he had discovered *the* essential solution of the problems of hereditary transmission. In further experiments[7] he soon found exceptions that only much later could be understood as irrelevant to the basic rules.

Perhaps the strongest impediment in the way of an acceptance of Mendel's pairs of genes by Darwin was his conviction that use and disuse of

[4] Mendel, Gregor, Versuche über Pflanzen-Hybriden, *Verhdlg. naturf. Verein Brünn* **4**: 3–47, 1866.

[5] Bateson, Wm., Segregation, *Jour. Genet.* **16**: 201–235, 1926.

[6] Letter of 15 April 1869 in Correns, Carl (edit.), Gregor Mendel's Briefe an Carl Nägeli. 1866–1873, *Abhdlg. mathem.-phys. Kl. Königl. Sächs. Ges. Wiss.* **29**: 189–265, 1905. English translation by Piternik, Leonie Kellen, and George Piternik in The birth of genetics, *Genetics* **35** (Suppl.): 1–29.

[7] Mendel, Gregor, Über einige aus künstlicher Befruchtung gewonnene Hieracium Bastarde, *Verhdlg. naturf. Verein Brünn* **8**: 26–31, 1870.

parts of the body of the parents repeated in a series of generations affects the corresponding parts of the offspring. Darwin's hypothesis of pangenesis was specifically designed to provide a basis for this supposedly established phenomenon.

VARIATION, GENETIC AND NON-GENETIC

Darwin's interest in inheritance was a derived one. His primary concern was with variation. In order to provide the raw material for evolution, deviations from a norm had to be postulated. Once their occurrence was demonstrated, it had then to be shown that they were inherited. Darwin had no difficulties in showing the ubiquity of variations between one individual and the next and between parents and offspring, nor did he fail to find numerous, albeit often erratic, instances of inheritance. He was able to formulate the deep insight that "transmission and development . . . [are] distinct powers."[8] He derived this generalization from the observation that a specific hereditary constitution may not express itself visibly although the existence of this constitution within the individual can be proven by the fact that it is transmitted from the ancestors of the individual to its descendants.

It remained for Johannsen to show much later not only that lack of visible variation among individuals was no evidence for genetic uniformity but also that presence of visible variation was no evidence for genetic variability.[9] Johannsen's analysis of the size variation of beans made it clear that there were two kinds of variations, genetic and non-genetic. Beans may differ in size because their hereditary make-up, their genotype, differs. Such size differences are inherited. They also may differ in size because they developed in different environments, as represented by factors in the outside world or by differences from one part to the other within the bean plant which bore them. These latter size differences proved to be not inherited. Often both differences in heredity and environment are jointly effective in making two beans vary from each other. Finally, the kind and degree of observable variation is often the same whether produced by genetic or non-genetic factors so that the visible measurable character, the phenotype, cannot be a guide to the genotype. What is true for the sizes of beans is equally true for the size of the body and the degrees of intelligence of man, and for a multitude of morphologic and physiologic attributes of animals and plants.

There were thus two types of variations, permanent and temporary. The latter could play no role in evolution—but the same appeared to be true for the former. While it was possible, as Johannsen demonstrated, to obtain permanently differing lines of beans by selection from an original population, this success consisted in no more than the sorting out of already present and constant genotypes. Thus, the fruitful analysis of variation had led to a deadlock in the genetic interpretation of evolution.

There were ways out of this impasse. The numbers of possible recombinations by means of sexual reproduction were shown to be inexhaustible. Here was a source of hereditary variants subject to selection and its evolutionary consequences. But to most biologists it seemed impossible that mere recombination of initially present genetic diversity would have led to such different forms as mammals and mosses, molluscs and molds. Perhaps this scepticism regarding the power of recombination was exaggerated. Only recently it has been suggested again that the astonishing similarity of biochemical processes in diverse species and the fundamental likeness of cellular types such as muscle cells, nerve cells, glands, and others, within widely differently constructed phyla of animals may betray a much more common genetic resemblance among the divergent products of evolution than has usually been granted.[10]

THE CAUSES OF VARIATIONS

In any case evolutionary genetic thought has followed a different path. The stability of the genetic material presumed by Mendel and demonstrated by him and by Johannsen was not absolute. DeVries had encountered in the evening primrose *Oenothera* a striking group of cases of hereditary changes which seemed to be based on intrinsic, permanent changes of the genotype.[11] Much later, many of DeVries' "mutations" turned out to be segregants from initially present genetic diversity of a complex type that is nearly unique in the biological world. Yet, while the original discovery proved to be of limited significance, the

[8] Darwin, *Variation, loc. cit.* **2**: 84.

[9] Johannsen, W., *Über Erblichkeit in Populationen und in reinen Linien*, Jena, G. Fischer, 1903.

[10] Stern, C., The role of genes in differentiation, *Proc. Intern. Genetics Sympos. Suppl. Cytologia*, 70–72, 1956.

[11] DeVries, H., *Mutationstheorie*, 2 v., Leipzig, Veit and Co., 1901.

general occurrence of mutations as elements of genetic newness became an established fact. Mutations were recognized as the prerequisites for evolution, prerequisites which furnished points of attack for such forces as selection, migration, and drift.

The causes of hereditary variation, of mutations, according to Darwin lie in the environment. Again and again he points to changed conditions of life as being responsible for variability. "If it were possible to expose all the individuals of a species during many generations to absolutely uniform conditions of life, there would be no variability," [12] he asserts. Only slightly less positive is his statement [13] that "we may infer that variability mainly depends on changed conditions of life." In general he does not attribute a directing force to the changed conditions of life. "We are thus driven to conclude that in most cases the conditions of life play a subordinate part in causing any particular modification." [14] Domestication, for example, has led to great variability in pigeons, horses, dogs, and other species who are relatively uniform in the natural environment. This variability goes in many different directions. The changed conditions of life are thus regarded as unstabilizers and the result is unspecific.

One direct connection between changed conditions and specific variations is accepted, although with qualifications. Darwin is persuaded that use and disuse of an organ which may strengthen or weaken its development can lead to genetic change so that the effects of use and disuse are inherited. "In many cases there is reason to believe that the lessened use . . . has affected the corresponding parts in the offspring . . ." though he finds "no good evidence that this ever follows in the course of a single generation" [15] and is aware of the fact that "it is very difficult to distinguish between the effects of the selection of indefinite variations, and the direct action of the conditions of life." [16] In order to explain the transmission to future generations of variations individually acquired by use or disuse, he formulates his hypothesis of pangenesis with its gemmules that are given up by all parts of the body and assemble in the germ cells.

The modern genetic interpretation of evolution has accepted Darwin's solution of the selection of indefinite heritable variations as being valid even for the evolutionary strengthening or disappearance of organs individually subjected to use or disuse. Neo-Darwinism sees no direct connection between the changes in a part brought about by use or disuse and the mutations in the genotype whose developmental effects may simulate those of use or disuse. This view grew out of numerous experiments with higher animals and plants which failed to demonstrate any direct causation of adaptive traits in the offspring by adaptations undergone by the parents, and out of the critical analysis of other experiments which were thought to have furnished such evidence but which were found wanting. The Neo-Darwinian view of evolution is in harmony with the general concepts of genetics which regard the genes of the germ cells as molecules whose structure represents a coded information which—translated into biochemical networks of activities—leads to the development of individual parts and functions. This scheme freely permits modification by adaptation and otherwise of the effects of the genic messages. It finds it difficult, however, to visualize how a modified effect can change the message itself in such a way that in a later generation it directs development spontaneously, without the modifying external causes, into the modified channel. This conceptual difficulty would and could be overcome if the facts of nature required it but no need for a general revision is apparent.

THE SPECIFICITY OF ADAPTATIONS

To the layman, and to some biologists also, one of the greatest difficulties in accepting the Darwinian and Neo-Darwinian interpretation of evolution is the high degree of specificity of adaptations. The human foot furnishes an often quoted example. A baby is born with thickenings of the epidermis on just those parts of its sole which will be exposed most to pressure and friction a year or so later when it begins to walk. It is remarkable enough that the human skin like that of other animals responds adaptively to use by thickening and hardening. One might have thought it sufficient if evolution had favored the establishment of this potentiality to form callosities under the influence of use. If the unborn child possessed skin of equal thinness all over his body the adaptive response would have taken care of forming the thickened skin later just where it was needed. Evolution, however, has gone beyond this establishment of a general potentiality for adaptive response of the skin. Already

[12] Darwin, *Variation, loc. cit.* **2**: 255.
[13] *Ibid.* **2**: 418.
[14] *Ibid.* **2**: 291.
[15] *Ibid.* **2**: 297.
[16] *Ibid.* **2**: 419.

in the embryo which is surrounded by the amniotic fluid and not subject to pressure differences there develop *specific* thickenings pre-adapted to later use.

How has this come about in the evolution of *Homo* from other mammals? Surely, the origin of the spontaneous development of specific thickenings must have been correlated with the evolution of the erect posture in man's ancestors. Darwin's interpretation of this fitting together of an inherited property of specific regions of the skin and the use of those regions in walking involved the inheritance of acquired characters. "It can hardly be doubted," he writes in *The Descent of Man*,[17] "that this [the thickness of skin on the soles of the feet] is due to the inherited effects of pressure during a long series of generations." When the prehominids first walked on their hindfeet, generation after generation, their soles responded adaptively to the new use of certain areas. Gradually, the continued use of these regions transformed their genetic constitution. It enabled them to send specific gemmules to the reproductive organs which built them into the germ cells so that the acquired characters became hereditarily fixed.

What was a legitimate hypothesis in Darwin's time is no longer an appropriate one for us. Genes are not representations of organs and tissues but are more like the individual letters of a book which in complex combinations arouse specific activities in the reader. The reader is free, under the influence of external events, to act independently of the initial suggestions of the book, or rather to interpret its message in a variety of ways. The letters and words of the book do not change on account of his activities. The modern geneticist has to look for a different interpretation from that of Darwin. He prefers to follow Darwin's general scheme of evolutionary agents rather than his obsolete hypothesis in which use and disuse act as causes of genic changes. The geneticist assumes the chance occurrence of mutations which regardless of the new erect mode of walking happen to lead to thickening of specific regions of the sole. Such mutations, he assumes, must have occurred many times before in the history of mammals. For ages they failed to become established since they lacked selective value. But when walking upright was initiated, then the formerly useless mutations acquired usefulness. Selection favored their retention and incorporation into the genotype of the new species.

If this train of thought strains credulity, its difficulties would seem to lie less in the process of establishment of the adapted genotype than in the assumption that there should exist mutations which *a priori* can single out limited and well-defined areas of the skin for their particular action. If the embryonic thickening of the human sole takes its origin independently of its use, the same must apply to the embryonic callosities on the outside of the forefeet of the warthog, an animal which digs in the soil with the back of its extremities. Could the warthogs likewise have possessed genotypes giving their soles thickenings in regions corresponding to the human foot but of no use to the warthog? Could men have originated with genotypes endowing the backs of their hands with callosities? Unhesitatingly, the answer is affirmative. The very existence of the inherited localized thickened regions of the sole or of the back of the forefeet is proof of the possibilities of astonishingly specific actions of genes. Likewise, observations on mutations occurring under controlled conditions furnish examples of localized action. Mutant genes are known in man which affect the number and size of his fingers. Some of these genes are rather unspecific in their effects. They introduce a general disturbance in the embryonic development of the hand and thus lead to abnormalities of all digits. Others are highly selective in their action. One gene may lead to duplication of the thumbs, another to the appearance of an extra little finger, a third to the shortening of the middle phalangeal bones of all fingers, a fourth to a shortening of the middle phalangeal bone of the index finger only. In the fly *Drosophila*, eleven pairs of single bristles are present on the dorsal surface of the thorax. They develop on specific places forming a pattern which is highly constant in flies taken in nature. Apart from variations in size these bristles are as similar among themselves as one hair is to another. And yet mutant genes exist which can single out specific bristles and suppress their development. There is no easy rule to such genic action. Gene A^1 may affect bristle 1, and gene A^2 bristle 2, but gene A^3 may be concerned with bristles 1 and 2, gene A^4 with bristles 2 and 3, and so on in many variations. Selection as practiced in the laboratory finds it easy to establish strains of flies which differ from one another by the possession of bristles at uniquely defined regions. Why should not selection occurring in nature do the same?

[17] Darwin, Charles, *The descent of man and selection in relation to sex* 1: 118, 2 v., London, John Murray, 1871.

THE EVOLUTION OF INHERITED ADAPTATIONS

Let us return to the human foot. Let it be granted that selection is responsible for the establishment of highly specific adaptive genotypes, in this case of the localized callosities. Selection could not have been active before the prehuman child reached the walking age. Would it not have been sufficient to establish a genotype which made the skin of the soles react suitably to the stimulus of walking? How did it come about that a genotype evolved which in each individual embryo produces the adaptive effect before the appearance of the cause which calls for adaptation? It might be admitted that selection may have favored some preformation of the callosities but it is difficult to see why such a preformation has to be laid down so many months before its use.

This problem has long been disturbing. Recently, Waddington has attacked it in a new fashion.[18] He began with a mental picture of development which consists of a surface, a "landscape" in which many grooves branch out from a distant point. These grooves or channels represent specific routes of development of the parts of an embryo. They are representations of the fact that development is only possible along well-defined alternative paths and that a route once entered is liable to impose restrictions upon consequent developmental behavior. Waddington terms this phenomenon the "canalization" of development.

The simile of the canalized landscape led Waddington to an interesting series of experiments. He exposed larvae of *Drosophila* to unusual external stimuli, such as heat shocks, and observed —as had been studied by others—that some of the individuals had responded by developing an abnormality in the venation of the adult wing. He selected these flies for further breeding and exposed their offspring to the same external treatment. Again he selected the flies who had responded and continued the experiment for many generations. It became obvious that more and more flies responded in the manner described. Clearly, the original group of flies was genetically heterogenous for various genotypes concerned with the ease of response to the heat treatment and the experiment had succeeded in selecting genotypes with high response.

This result was expected and not of unusual interest. In Waddington's terms, selection had assembled genes which deepen the channel for temperature response. The new aspect of the experiment was that the picture of the deepened response channel had made Waddington think that the highly responsive flies might even without the temperature shock follow the developmental groove toward abnormal venation. This indeed was found to be true.

Applied to our example of the human sole, the *Drosophila* experiments would mean (1) that the prehuman Primates which began to walk upright underwent selection for suitable skin response of the individuals to the external stimulus provided by their new mode of life and (2) that the well responding genotypes were intrinsically of such a nature as to bring forth the spontaneous appearance of the foot adaptations. Waddington has called this transformation from individual response to autonomous production "genetic assimilation."

If Waddington's concept of the canalized landscape of development had the heuristic value of suggesting the *Drosophila* experiments just described, it may still be considered whether a high degree of response and the appearance of the trait in the absence of the external stimulus are correlated for intrinsic reasons or whether some other mechanism may have been involved. An alternative hypothesis known under the designation "Baldwin effect" has long been discussed.[19] It assumes in the case of the evolution of the foot sole that in addition to the somatic acquisition of callosities, mutations for their autonomous development happened to occur and that they were selected under cover of the externally induced skin thickenings. This explanation, however, does not make it clear why selection should have favored a genetically anchored system of callosities when their individual acquisition was already assured by the individual reactivity. This problem does not arise for another hypothesis which can account for the success of selection for high individual response to the external stimulus as well as for the ensuing spontaneous genetic assimilation to autonomous development of the traits.[20] According to this hypothesis a range of genotypes has existed among the ancestors of man which

[18] For a general discussion and earlier references see Waddington, C. H., *The strategy of the genes*, New York, Macmillan, 1957.

[19] Waddington, C. H., The "Baldwin effect," genetic assimilation and homeostasis, *Evolution* **7**: 386–387, 1953.

[20] Stern, C., Selection for subthreshold differences and the origin of pseudoexogenous adaptations, *Amer. Nat.* **92**: 313–316, 1958.

endowed their individual bearers to a varying degree with the ability to respond by specific callus formation to the new uses of the foot sole. The hypothesis, in oversimplified form, begins with the fact that many genes have only a slight effect if they are present in single dose but a strong effect in double dose. If, for instance the gene pair *AA* did not lead to the spontaneous production of specific callosities while the combination *AA'* implied a slight tendency toward this trait, then *A'A'* might well cause its invariable appearance. In a population in which the gene *A* is highly abundant, and *A'* correspondingly rare, most individuals would be *AA*, a few *AA'* and practically none *A'A'*. Be it assumed that the *AA'* individuals will under pressure form callosities easier than *AA* individuals. They will then have been favored by selection and their number will increase. The higher frequency will lead to crosses between *AA'* males and females, and as a necessary consequence of Mendelian segregation one quarter of their offspring will be *A'A'*. This latter genotype is the very one which causes the spontaneous appearance of the callosities.

There are many variants possible to this hypothesis but they agree in making the spontaneous development of a trait the automatic result of selection for its appearance under special conditions. If one wishes to retain the term "genetic assimilation" for the sequence of events suggested here one would have to redefine it. Instead of its signifying selection for genotypes that deepen a channel of response to special stimuli until the channel is there "by itself," the special stimuli would be no more than means of making available to selection genotypes that are not recognizable normally. In this view genetic assimilation would constitute the ordinary processes of gene combination which can assemble stronger genotypes in the progeny of weaker ones.

THE "BONUS PRINCIPLE"

Apart from its aid in the understanding of variations and their transmission, the hypothesis offered for the genetic fixation of variations which at first appear individually under special conditions of life may be cited as an example of what somewhat flippantly can be called the "bonus principle."[21] By this I refer to the phenomenon that Nature gives more than what seems required of her. The theory of Mendelian recombination explains many phenomena of the inheritance of genes. It has led, as any fruitful theory, to predictions of new findings. But it certainly was not obvious that it also could furnish a basis for the process of genetic assimilation.

For another biological example one might think of the wonders of regeneration of lost parts and the formation of twins and quadruplets from half and quarter embryos. In order to account for these facts, Weismann and others saw themselves forced to think of complex schemes, based on selective advantages of retaining spare genes in otherwise specialized cells. We now know that regulating processes are possible because each single cell carries a copy of the whole blueprint of the individual's genotype. The simple facts of mitosis which assure this presence of like chromosomes in all cells of the body carry as a bonus the possibility of regeneration and twinning.

A third case in point concerns the walking behavior of various animals, among them the spiderlike harvest men and of crustaceans, who have experimentally been deprived of one or more of their legs.[22] The unmutilated harvest man moves his eight legs in a well-defined sequence that results in a straightforward motion. In individuals with seven, six, or still lower numbers of legs the sequence of motion is rearranged automatically, without a learning process, in such a way that maximum mechanical fitness is retained. With different legs removed, a new and different task is posed in each case. It is fulfilled perfectly. Apparently, the neural mechanisms involved in normal locomotion have a built-in principle which can also take care of abnormal situations. This behavior can hardly have evolved in connection with losses of individual legs or combinations of them. Rather it must be immanent in the normal mechanism.

These considerations apply in a much wider realm. Could it have been foreseen when our part of the astronomical universe was in the primeval state that its atoms would aggregate to form suns and planets with mountains and seas? What observer of the carbon atom could have predicted that its elementary properties would make possible the origin of infinite varieties of compounds and with them of life? The immanence in the universe of potencies far beyond those foreseeable by the human mind is apt to raise in us feelings of humility as well as to bring with them a measure of consolation.

[21] This designation arose out of a personal discussion with the late D. R. Charles.

[22] Bethe, A., and E. E. Fischer, Die Anpassungsfähigkeit (Plastizität) des Nervensystems, *Handbch. d. normalen u. pathol. Physiol.* **15**(*2*) : 1045–1130, 1931.

DARWIN'S VIEWS ON VARIATION UNDER DOMESTICATION IN THE LIGHT OF PRESENT-DAY KNOWLEDGE

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I. INTRODUCTION

NOWADAYS geneticists seldom read Darwin in the original. The reason for this is certainly not that his production has lost its importance and is merely of historical interest. On the contrary, the essential points are still, and will always be, of such fundamental importance that they are indispensable for every geneticist and belong to the basic elements of his scientific education.

However, it still pays to go back to Darwin's works not only for historical reasons but also because in many respects they are surprisingly modern. They contain such a richness of empirical data that most geneticists will find several points with important bearings on their own fields of work. As is well known, Darwin had a remarkable ability to assemble and collect empirical data, relevant to his problems, and survey these data in a masterly way. It is also very striking that Darwin himself was a great empiricist, who never

hesitated to start comprehensive series of experiments, with plants as well as animals, in order to shed new light on some problem of particular interest to himself.

Though Darwin had a keen critical sense, we can see that in some cases he was misled by erroneous information from workers less critical than himself. The influence of Lamarck and his school is very obvious and lies behind Darwin's inability to distinguish between purely environmental modifications and changes caused by alterations in the hereditary constitution. In this connection the fundamental importance of Mendel's results becomes especially clear, and also when Darwin discusses reversions and other kinds of variability we feel strongly how tragic is the fact that he probably never heard of Mendel's results or realized their importance.

Another feature, which strikes the geneticist when reading Darwin's works, is that he saw and clearly described almost all genetical phenomena of fundamental importance although in most of these cases he was unable to give any plausible explanation of the observations made. Thus, for instance, he clearly reported cases of mutation, dominance, monohybrid segregation, heterosis, inbreeding degeneration, increasing morphological uniformity in inbred lines, genetically conditioned self-incompatibility, and so on.

Even a foreign reader, whose knowledge of the English language is inadequate, cannot fail to be impressed and stimulated by Darwin's stylistic mastery. His way of writing is exceedingly clear, and he presents the points of importance in a direct manner, without the heavy pseudo-scientific turgidity or the over-intelligent stylistic extravagances which may otherwise burden the reader.

When trying to compare Darwin's ideas and our own concerning variation under domestication, it is first necessary to state and define Darwin's views as precisely as possible. The present writer has tried to do this in five short chapters, which finish with comments indicating our present conceptions. After the fifth chapter, which states the essential conclusions of Darwin concerning the origin and development of the domestic species, there are two chapters giving some information on recent results and present-day views on the origin and development of domestic animals and cultivated plants. As this field of research is, indeed, very comprehensive, my presentation is necessarily fragmentary.

It has not been possible to limit this paper strictly to variation under domestication without touching on Darwin's views concerning other fundamental problems such as inheritance and variation in general; and, indeed, as is well known, Darwin, in the first place, founded his general views on the evidence obtained from the domestic species.

Darwin's main work in this field is represented by the two volumes published in 1868, *Animals and Plants under Domestication*. The preceding great work, which we now celebrate, *On the Origin of Species* (1859) contains the essential points of Darwin's observations and conclusions on variation under domestication. In this respect, however, *On the Origin of Species*, may be considered a preliminary communication to the full report published nine years later. In a third work, of 1876, Darwin has concentrated on a particularly interesting part of the great field of research dealing with variation under domestication. In this book he describes the results of comprehensive experiments on the effects of cross-, and self-fertilization in plants.

II. EFFECTS OF ENVIRONMENT

1. INDUCED ADAPTIVE MODIFICATIONS WHICH ARE SUPPOSED TO BE INHERITED

According to Darwin, species, when domesticated, fail to transmit their original form and start to vary, this variation being caused by the variable conditions of life to which the domestic species are exposed. The correlation between the living material and the external conditions is considered to be very close and Darwin discusses whether the domestic productions would ever become so completely habituated to the conditions under which they now live as to cease varying.

Being influenced by Lamarck, Darwin is convinced that the biological variation is chiefly conditioned by direct influences of the environment on the organisms, believing that the changes thus induced become inherited. Hardly any kind of change affects either parent without some mark being left on the germ, says Darwin, and also the effects of long-continued use or disuse of parts are supposed to be inherited. As evidence on this point Darwin states that certain parts of the skeleton in our anciently domesticated animals have been modified by the effects of increased or decreased use. Darwin also says that there is no doubt that the evil effects of long-continued ex-

posure to injurious conditions are sometimes transmitted to the offspring. He finds, however, that mutilations are without inherited result and also states that the custom of some primitive tribes of man to change the shape of their infants' skulls by pressure has no influence on skull shape in the offspring.

A peculiar fact to puzzle Darwin was that the influence of changed conditions seems to accumulate, so that no effect is produced on a species until it has been exposed during several generations to continued cultivation or domestication. Then, gradually, new characters start to appear which sooner or later may become fixed and inherited. On the other hand extremely slight changes in the conditions of life often suffice to cause variability, and as an example Darwin mentions the specific galls induced in plants by various species of insects.

With regard to the influence of a changed environment Darwin considers the possibility of so-called *definite action*, which would imply that all or almost all individuals after a number of generations are hereditarily modified in the same manner. Thus, in this way a new sub-variety would arise without the aid of selection. As a good example Darwin mentions that several varieties of maize when brought from the hotter parts of America to Germany were transformed in the course of two or three generations. He also discusses the average adaptive differences between American species of trees and their European relatives and is inclined to ascribe at least part of these differences to the long-continued action of the different climates.

It is interesting that Darwin, just as some recent workers in the Soviet Union, believed that the action of habit may in the course of a very few generations induce a conversion of summer wheat into winter wheat and *vice versa*. Changed conditions would also have the power of evoking long-lost characters as in the case of some feral animals, which are said to revert to the wild type as they leave the conditions of domestication.

As is already well known from elementary textbooks Darwin's views on the action of the conditions of life on the organisms gave rise to his hypothesis of pangenesis, according to which every part and every cell of the body throws off minute gemmules, which are transmitted by the sex cells to the following generation. Now, in variations caused by the direct action of changed conditions the tissues affected are supposed to throw off modified gemmules, which are transmitted with their newly acquired peculiarities to the offspring. Several generations may be needed before the new modified gemmules are at last sufficiently numerous to bring about a definite change in the organisms. This hypothesis is ingenious, and if it had been true, it would certainly very well cover the observed facts gathered by Darwin.

Darwin also discusses which kinds of environmental action are most effective in causing inherited modifications. Andrew Knight attributed the increased variation in domestic species to a more abundant supply of nourishment or to a more favorable climate than that natural to the species. Darwin says that a change in the nature of food is scarcely responsible for the increased variability but considers an excess of food to be most powerful; he suggests that a superfluity of nutrient fluids might disturb the due and proper action of the reproductive organs. In support of this view he cites a certain raiser of seeds in different species of cultivated plants who had found that the best way of keeping true stock of any one kind of seed was to grow it in poor land without dung. Otherwise the excess of nutrients will give rise to an undesirable variability in the material.

The increased amount of nutrients available under domestication would not only explain the increased tendency to variation but also the increased degree of fertility, which is generally characteristic of domestic animals in comparison with their wild relatives. However, in some cases animals and plants, when removed from their natural conditions are rendered infertile. This may sometimes be advantageous as the useful parts of the organism may gain from this sterility and become better developed. Darwin noticed that such sterility is not infrequent among highly cultivated plants and believes the cause to be excess of food and other unnatural conditions.

As we have seen, changed conditions often are supposed to act on the organisms and to induce heritable changes independently of the reproductive organs. On the other hand we have heard that the sexual system is easily affected by changed conditions so that it is often rendered impotent. When not so seriously affected the reproductive organs are supposed to fail in their proper functions of truly transmitting the characters of the parents to the offspring. On the basis of the

pangenesis hypothesis, it may be imagined that in such cases the gemmules are aggregated in an irregular manner.

Darwin repeatedly stresses that, although changes in the environmental conditions induce variability, the kinds of new characters appearing are much more conditioned by the particular constitution of the material than by the nature of the changed conditions. In most cases the conditions of life play a subordinate part in causing any particular modification. "Each trifling variation is governed by law and is determined in a much higher degree by the nature of the organization than by the nature of the conditions."

2. EFFECTS OF CHANGED CONDITIONS COMBINED WITH SELECTION

Darwin finds it difficult to distinguish between the effects of the direct action of the conditions of life and the effects of the selection of indefinite variations. Thus, changed conditions should not only have direct and heritable effects on the organisms but also induce an infinite and fluctuating variability. This gives a polymorphic material on which natural selection may work, and under such circumstances Darwin is uncertain whether well-marked races have often been produced by the direct action of changed conditions without the aid of selection.

He has observed the marked polymorphism among seedlings of various fruit trees, regarding this as an example of constantly recurring variability induced by the conditions of life. Owing to prolonged vegetative propagation fruit tree varieties have been exposed to widely diversified conditions. Darwin is puzzled that habit, however much prolonged, has rarely produced any effect on plants propagated vegetatively and says that it apparently acts only through successive seminal generations. He is aware, however, that in these seminal generations, just as in animal material, the effect of the environment will also be influenced by selection.

3. ACCLIMATIZATION

Darwin repeatedly returns to the important problem of acclimatization, which from a practical point of view is most urgent in plants but which it also met with in domestic animals. He knew that with the varieties of many plants adaptation to climate is often very close. This is, for instance, the case with the maize varieties in North America, where the northern varieties flower and ripen their seeds progressively earlier than in the south. Seedlings of *Pinus sylvestris*, raised from seed from the continent and from the forests of Scotland differ much in winter hardiness, and marked differences in hardiness are also met with in different varieties of fruit trees. Thus, the many fruit trees which are so well fitted for the hot summers and cold winters of North America give poor results in the British climate. Numerous other examples of acclimatization in plants are given, and it is demonstrated that similar differences also occur in various kinds of animal material.

Darwin thinks that although long-continued habit has a certain bearing on acclimatization, yet the spontaneous appearance of constitutionally different individuals is a far more effective agent. His general conclusion is that under natural conditions new races and species become adapted to widely different climates by spontaneous variation aided by habit and regulated by natural selection. Darwin considers that man has done little in the acclimatization of domestic animals and cultivated plants. Nevertheless, it is already evident from the examples given by him that in many cases acclimatization and ecological differentiation have spontaneously occurred during the long period of domestication of various animals and cultivation of useful plants.

4. COMMENTS

With regard to the effects of environment on animals and plant present-day views differ fundamentally from those of Darwin. The basic difference is that Darwin was unable to distinguish between phenotype and genotype, nor did he know the difference between purely environmental modifications and variations conditioned by a change in the hereditary constitution. Our present knowledge in this field is in the first place based on Mendel's discovery of stable units of heredity, later called genes. It was also Mendel who first realized that individuals may have the same appearance and yet differ with regard to their hereditary constitution. On account of dominance, an individual *Aa* looks like *AA*, but, nevertheless, the offspring of these individuals will be quite different. Johannsen further clarified the distinction between the inherited constitution, the genotype, and the properties of an individual, representing its phenotype. Johannsen also taught us that reaction norms rather than characters are

inherited, and that the visible or in other ways analyzable properties of an individual, the phenotype, is always the result of an interaction between the genotype and the environment.

Another fundamental difference between our views and those of Darwin is that he did not know the mechanisms of recombination and did not know that hereditary changes are of two kinds, those depending on recombination of already existing genes and those caused by mutations, sudden changes in the genotype, which do not represent recombinations. As every student of genetics now knows, the concept mutation also covers several different phenomena, from changes in the number of chromosomes to point mutation, small changes in the large molecules constituting the genes.

Darwin's first thesis, when discussing variation under domestication, is that *species when domesticated start to vary*. Though there is a slight possibility that some factor or factors in the changed conditions of life, such as special foodstuffs or a changed endocrinic balance, may tend to increase mutability, the observed increase in variation is essentially due to quite other causes. As animals and plants, also in the wild state (with the exception of spontaneously self-fertilizing plants), are heterozygous for numerous genes, segregation of deviating individuals will incessantly occur, but as a rule the markedly deviating segregates will not be viable in nature but will disappear at an early stage. The same is also true of individuals carrying new mutant genes.

Under domestication, on the contrary, conditions are more favorable for the survival of deviating types, some of which may be useful for man and, hence, consciously or unconsciously selected. Thus, man preserves part of the variants which in nature would have no chance of survival. This explanation gains further strength from the fact that many of the properties of domestic animals and plants are more or less clearly abnormal or even pathological. To illustrate this point we may, for instance, refer to ornamental plants with filled flowers, to the various peculiar fancy breeds of pigeon and gold fish or to the so-called rex factor in the domestic rabbit. Gradually it was realized that this factor does not only induce a valuable change in the type of hair coat but has also other less desirable effects. The gene in question probably causes a specific disturbance in the endocrinic secretion. Secondarily, this causes not only a change in the hair coat but also a more sensitive constitution as well as metabolic disturbances. Therefore, rex rabbits have a lower weight at birth than normal rabbits; the young have a higher mortality and are especially liable to diseases in the respiratory ducts and to rachitis and certain eye diseases. The rex rabbits also have a decreased ability to utilize their food.

It should be observed that similar conditions also prevail in man. We are polymorphic, and part of this polymorphism is certainly due to the fact that we are self-domesticated. The far-reaching control of our environment has enabled us to exist also in cases where our constitution is hampered by serious handicaps which would have been lethal or sublethal under primitive, natural conditions.

Thus, Darwin's thesis that species when domesticated start to vary is essentially or entirely wrong. Variation is not increased but the changed environment allows the survival of many types of interest to man, but which in the wild state are removed by natural selection.

As Darwin believed that domestication leads to an increased degree of variation, he looked for the causes of this increase and states that *the variable conditions of life and especially excess of food are most powerful as causes of increased variability*.

We can agree with him that such factors may lead to marked modifications, but we do not accept his statement that *the changes induced in this way become inherited*. An overwhelming amount of evidence has demonstrated that this is not the case, that neither the effects of use or disuse of an organ, nor the evil effects of long-continued exposure to injurious conditions are, as Darwin believed, transmitted to the offspring. A rich supply of food may of course be a favorable factor for the survival of variants with decreased vigor which would not survive the test of natural selection; and in this way variability would indirectly be increased under domestic conditions.

Darwin's observation that *the influence of changed conditions accumulates*, no effect on the progeny as a rule being evident in the first generations, does not depend on modified gemmules gradually reaching a threshold value sufficient for visible manifestation but may now be explained in a different way. As the frequency of spontaneous mutation is generally low, several generations and a fairly large material may be required before a clearly deviating type will appear. Such de-

viating types may also be produced by recombination of genes already present in the starting material; but, especially if the material available is limited in number, segregation of homozygous recessives or more complicated segregants, involving more than one pair of genes, may not appear in the first generations. Such segregants are more likely to occur, when a certain degree of inbreeding is practised, as is often the case in domestic species. The correctness of this interpretation is well supported by the experience gathered in species which have recently become domesticated, and in which it has been possible step by step to follow their variation under domestication (*cf.* below p. 205).

Darwin believed that excess of food and other unnatural conditions disturb the due and proper action of the reproductive organs and that in extreme cases this may lead to sterility. As an example he mentions several seedless varieties of cultivated plants, which consequently are propagated vegetatively, e.g., certain varieties of pears, pineapples, bananas, sugarcane, etc. Darwin could not know that in most of these cases sterility is due to an unbalanced chromosome constitution and especially to triploidy or higher degrees of polyploidy. On the other hand it is correct that in domestic animals changed conditions may affect the sexual system, bulls, for instance, easily becoming transiently sterile when transferred to a new environment. This, however, certainly does not tend to increase variability in the offspring of individuals thus affected.

Darwin was much puzzled by the fact that habit rarely produces any effect on plants propagated vegetatively, not realizing that the cause of this is the constant genotypical constitution, the effects of which are only to a slight degree modified by various environmental conditions. In striking contrast to the constancy of vegetatively propagated fruit trees is the strong polymorphism in the offspring raised from seeds. We know now that this strong variability is not, as Darwin thought, the result of various environmental influences to which the mother individual has been exposed. Instead, it is caused by a strong heterozygosity, which certainly has been continually increased by new mutations. In the offspring of triploid varieties there is not only genetic segregation but also variability caused by variable and largely aneuploid chromosome numbers.

Though Darwin believed that variability is exclusively *caused* by environmental influences, it should be emphasized that he stresses the point that the constitution of the organisms will largely decide *which kind of change* will be induced. Thus, the organisms have special constitutions which, though easily affected and changed by environmental influences, have a certain limited degree of independence.

Darwin hesitated as to whether "definite action," without the aid of selection, ever occurs. We now know with certainty that definite action (a permanent change of a whole group of material, exclusively caused by a changed environment) does not occur at all. The individuals may certainly be modified, but permanent changes only occur as a result of recombination and selection.

Darwin realized that among the highly variable seedling offspring from fruit trees there is ample opportunity for selection, and this observation influenced his views concerning the factors involved in the process of *acclimatization*. His conclusion that acclimatization is accomplished by spontaneous variation, aided by habit and regulated by natural selection, is almost entirely correct. The incorrect part is "aided by habit," as this statement not only implies individual, non-inherited modifications, which certainly also play a role in acclimatization, but also the gradual fixation and inheritance of such changes. If Darwin had better known the different mechanisms involved in spontaneous variation, his views on acclimatization would have been still more adequate.

On the foundation laid by Darwin other workers have at a later stage succeeded in still further elucidating the problem of acclimatization and adaptation. Without going into details with regard to this wide field of research I wish to point out a few investigations of special importance.

In 1911 Nilsson-Ehle read a paper at the IVth International Conference of Genetics in Paris on acclimatization in wheat. He showed that winter hardiness in the land varieties of wheat strictly corresponds to the climate of the different regions where these varieties are cultivated, and that this parallelism is not due to "direct action" but to selection of biotypes with a sufficient degree of hardiness. Just as other quantitative characters, winter hardiness was shown to be conditioned by several or many genes, which give a complicated segregation after crossing, but which, nevertheless, essentially follow the laws of inheritance discovered by Mendel.

In cultivated plants a surprisingly close corre-

spondence between climate and genotypical constitution has later been found, not only in wheat but also in many other species. In Sweden where the differences in climate between various parts of the country are very pronounced, it was therefore found necessary to carry out plant breeding with the help of breeding stations spread all over the country. As a rule, successful results can only be obtained if selection among a genetically heterogeneous material is carried out in the local region in which the product of breeding is going to be used. Only in this way is it possible to obtain products with a sufficiently good adaptation to climate and edaphic conditions.

The general occurrence of genotypical adaptations to various environments was further studied in wild plants by Nilsson-Ehle's pupil Turesson (*cf.* Turesson, 1922, 1923, 1925, 1930, 1936). By transplantations and crosses he demonstrated the general occurrence of so-called ecotypes within the species, the ecotypes representing groups of biotypes genetically adapted to certain environments. Especially when the environment is discontinuous on account of edaphic differences, such as those between mountain and lowland or between forest region and seashore, the ecotypes may be quite distinct. In other cases, when differentiation is caused more by climatic differences, such as temperature or day length, the ectotypes may gradually be transferred into ecoclines, representing quite continuous transitions between various extremes.

Later on similar investigations have been carried out by many others. Special attention should be paid to the work of Clausen and collaborators in California (*cf.* Clausen, Keck, and Hiesy, 1940, 1945, 1948).

The combined evidence obtained by all workers in this field clearly shows within the species a far-reaching differentiation which represents genotypic adaptations to different kinds of environment In some species this differentiation is purely genetic and based on recombination of multiple genes (also called polymeric genes or polygenes). In other groups differences in the number of structure of the chromosomes may be involved, and in such cases intraspecific polyploidy is especially frequent (*cf.* Müntzing, 1936). As demonstrated particularly well by Clausen (1951), there are continuous transitions between differentiation, which is typically intraspecific, and those cases in which it is more justified to speak of species differences.

Though it is now settled beyond doubt that acclimatization and other adaptations to different conditions of life are established by selection of individuals with suitable constellations of multiple genes for various important quantitative characters, it is also quite clear that every individual has a more or less pronounced degree of adaptive plasticity. But in contrast to Darwin we now know that such environmental modifications leave no mark on the offspring. Inherited acclimatization and adaptation *exclusively* result from selection in a material varying genotypically.

III. EFFECTS OF CROSSING AND INBREEDING

1. INCREASED VIGOR AND FERTILITY BY INTERCROSSING

Already at the time of Darwin it was realized that crosses between different individuals, varieties or species as a rule lead to hybrids with an increased degree of vigor. As early as 1799 Knight (according to Darwin) emphasized the importance of cross-fertilization for plant vigor, and Darwin confirms that great good is derived from the crossing of plants. He regards this as a great law of nature and discusses the various ingenious methods by which cross-fertilization is secured in the plant kingdom.

As for animals, it had been found that cross-bred individuals are generally of large size and vigorous and hence, already a hundred years ago, they were raised in great numbers in several parts of England for immediate consumption. Their merit was so fully recognized that at fat-cattle shows a separate class was formed for their reception. It was also known that cross-bred chickens were especially hardy and easily reared. It was equally well known, however, that for breeding purposes these products of intercrossing were utterly useless. Nevertheless, the good effects of intercrossing were utilized in cattle breeding work by the common practice of "infusing new blood" by procuring bucks from other parks. In sheep-breeding a certain Jonas Webb had the good idea of keeping five separate families to work on and to intercross in order to "retain the requisite distance of relationship between the sexes." A certain Mr. Spooner asserted that there is a direct pecuniary advantage in judicious cross-breeding.

The increased vigor and fertility of cross-bred individuals is also evident from a statement by Darwin to the effect that in many crosses mongrels have been found to increase more rapidly

than pure parent-breeds. He also states that the effects of crosses are favorable when the individuals combined are either innately of different constitution or have been differentiated by exposure to dissimilar conditions. The latter statement shows to what extent Darwin considered the inherited properties to be controlled by environmental conditions. He also says that just as a change of environment is stimulating to any creature so the germ becomes more stimulated and this results in a more vigorous individual, if the male element comes from a distinct individual.

2. CROSSING AS A CAUSE OF REVERSION AND VARIATION

By reversion Darwin means the sudden appearance of individuals with characters which were present in some more or less remote progenitor. These characters have been latent for some time and then unexpectedly reappear. Darwin points out that crossing is evidently a potent means of inducing reversion and believes that the act of crossing in itself tends to bring back long-lost characters. More precisely, crossing causes a disturbance in the organization, which is upset in such a way that characters so far hidden get a chance to reappear. Sometimes reversion may occur already in the immediate progeny of a cross, which in more modern language means that F_1 after a cross between two different homozygous recessive types is of wild type. In this connection Darwin makes the now amusing remark that "such cases of immediate reversion to a primitive type remind us of statements on the degraded state and savage disposition of crossed races of man." He adds, however, that this savage condition may also depend on the unfavorable moral conditions under which such human mongrels generally exist.

Darwin is well aware that crossing may lead to excessive variability of the crossed offspring but says that this variability is due to the principle of reversion. He mentions that Naudin and some other authors believe that crossing is the chief cause of variability and also points to the experience of floriculturists. According to their experience the first generation of a cross is generally uniform but subsequently an almost infinite diversity of characters arises. Darwin has not been able to grasp the full significance of such facts and tries to distinguish between variability depending on the commingling of the characters derived from the two parent forms and the somewhat abnormal variability induced by the act of crossing. It is also very noteworthy that he himself made a cross between a zygomorphic and a peloric strain of *Antirrhinum majus* and found the primary hybrids to be all zygomorphic, giving in the next generation a total of 88 zygomorphic and 37 peloric individuals. This is a typical monohybrid segregation, but Darwin's attention was focused on the so-called prepotency of transmission. Here he is puzzled by the fact that the tendency to pelorism appeared to gain strength by the intermission of a generation and prevailed to a large extent in the second set of seedlings. The general conclusion from these observations is that the subject of prepotency is extremely intricate.

3. PRODUCTION OF NEW RACES BY CROSSING

In the middle of the nineteenth century, breeders, though not averse to a single infusion of foreign blood, were almost universally convinced that the attempt to establish a new race, intermediate between two widely distinct races, was hopeless. The reason for this conviction was that offspring of the generally uniform primary hybrids during many generations had been found to be astonishingly diversified. For that reason the breeder was driven to despair and concluded that he would never get an intermediate race. Darwin realized, however, that patience alone was necessary, and that after six or seven generations the hoped-for result would, indeed, be obtained. Thus, he concludes that crossing between two breeds sooner or later gives an intimate blending but not so soon as might have been expected.

With plants which can be multiplied by buds and cuttings it was known that hybridization had done wonders as in the cases of roses, rhododendrons, pelargoniums, calceolarias, and petunias. Nearly all of these products could be propagated by seed but extremely few or none at all came true by seed.

4. UNIFORMITY WITHIN A RACE BY MEANS OF FREE INTERCROSSING

Before 1868 Darwin was not familiar with the occurrence of spontaneous self-fertilization in higher plants and says that he does not know any single species in which the structure ensures self-fertilization. In his book of 1876 he mentions a few cases of this kind, but, he has no conscious knowledge of constancy resulting from homozygosity in non-inbred material. Another

way to an apparently high degree of uniformity is repeatedly stressed by Darwin, namely free intercrossing within a domestic race or smaller population. Half-wild cattle, each representing a slightly different type, occurred at that time in several British parks, and the uniformity in each population was considered to be due to free intercrossing without any intentional selection and breeding. A similar situation, though on a large scale, was known to occur in the Argentine where the semi-wild cattle and horses had a perfect opportunity for free intercrossing without any interference by man and therefore represented markedly uniform though specific types.

5. EFFECTS OF INBREEDING

In Darwin's time the deleterious effects of close inbreeding (by Darwin called "interbreeding") were well known to all animal breeders. To Darwin therefore it was a great law of nature that long-continued close inbreeding is injurious, whereas crossing, on the contrary, is highly beneficial. The consequences of close inbreeding carried on for too long are, according to Darwin,

> loss of size, constitutional vigour and fertility, sometimes accompanied by a tendency to malformation. Manifest evil does not usually follow from pairing the nearest relations for two, three or even four generations; but several causes interfere with our detecting the evil—such as the deterioration being very gradual, and the difficulty of distinguishing between such direct evil and the inevitable augmentation of any morbid tendencies which may be latent or apparent in the related parents.

With plant material Darwin has made extensive comparisons between offspring raised after crossing and selfing. The latter category was often found to be remarkably inferior in vigor and Darwin, therefore, had good reason to assume that also in plants inbreeding was deleterious. However, the experience from plant material was less complete, little being known of the evil effects of long-continued close inbreeding.

In domestic animals Darwin had observed that when a breed, from not being valued, is kept in small numbers its extinction follows sooner or later. This was ascribed either to accidental causes of destruction or to the evil effects of close inbreeding.

In spite of the obvious risks of inbreeding this way of breeding was generally practiced in work with domestic animals because it had been observed to lead to "retention of character." Thus, if not carried to an injurious extreme, inbreeding, in a desirable way, tended to fix the characters of each breed. Thus, not only the evil effects of inbreeding were well known at Darwin's time but also the homogeneity and constancy of character in each special stock. It must also have been more or less clear that inbreeding leads to differentiation between different groups of material. Darwin states that the half-wild cattle in several British parks, owing to not having been mingled and crossed during many generations, differ in a slight degree. He believes that inbreeding degeneration can be checked if the related individuals are separated during a few generations and exposed to different conditions of life. In that way the different environments would soon reshape the constitution of the animals and bring about a sufficient degree of dissimilarity. This suggestion clearly shows to what an extent the conditions of life are supposed to act on the individuals and how the induced changes are presumably transmitted to the offspring.

6. COMMENTS

To a surprisingly high degree Darwin and his contemporary animal breeders were familiar with the favorable effects of crossing, and it is especially interesting to learn that the increased vigor of F_1 hybrids between different populations or races was even utilized commercially, such animals being produced for immediate consumption. Darwin states that a good result of such intercrossing is obtained, if the individuals combined are either innately of different constitution or have been differentiated by exposure to dissimilar conditions. Here we meet again the Lamarckian belief that environmental modifications are hereditary and that in consequence the transmitted hereditary properties are changed if the individual is exposed to a new environment. Such an effect, it is true, may be obtained by selection after a number of generations, but what Darwin had in mind was certainly the immediate action of the environment.

To Darwin, *reversion* (the reappearance of characters from earlier generations) was an important concept, almost as important as inheritance itself. He found that crossing is a potent means of inducing reversion and believed that the act of crossing in itself tends to bring back long-lost characters. Thus, crossing was regarded as a disturbance in the organization which upsets the constitutional equilibrium in such a way that latent

characters may reappear. Darwin's views in this respect, and his failure to grasp the mechanism behind the monohybrid segregation in *Antirrhinum*, observed by himself, make it easier for us fully to realize the greatness of Mendel's results. If Darwin had seen Mendel's paper, which was published in 1866, two years before his own book on *The Variation of Animals and Plants under Domestication*, he would have learned that variability after crossing is not due to a disturbance of the sexual functions but to recombination of a number of stable units of heredity. This mechanism also easily explains the peculiar reversions (whether occurring in F_1 or later generations) which puzzled him and which he tried to explain by his hypothesis of pangenesis.

In other respects, however, we can agree with Darwin concerning the effects of crossing, e.g., with his statements that crossing between two breeds sooner or later gives an intimate blending and that uniformity within a domestic race is obtained when there is an opportunity for free intercrossing. Both these statements are based on sound observation and experience without any special attempts to theoretical explanations. With regard to the first statement, it is true, we do not now consider that a new more or less intermediate race selected in the offspring of a cross between two other races represents a real blending or fusion between the hereditary constitutions. We would rather say that the characters of the two races are mainly conditioned by multiple genes, and that recombination of such genes will generally result in more or less intermediate products.

The other statement, that free intercrossing results in uniformity, may seem more peculiar, especially to plant geneticists working with homozygous material of autogamous species. In such material crossing leads to variation, in marked contrast to the constancy of the homozygous parent types. The uniformity within a cross-fertilizing population with panmixis is certainly not complete, every individual having its special genotype and phenotype. Nevertheless, what Darwin had in mind was the contrast between such a material and the products obtained when selective mating and a certain degree of inbreeding had been carried out for some time. By such a procedure an apparently uniform population will be differentiated into various more or less distinct lines.

In Darwin's time the effects of inbreeding were already very well known from the experiences of animal breeders; and inbreeding, in order to obtain uniformity for certain valuable characters, had, indeed, been practiced for more than a hundred years. The pioneer in this field was Robert Bakewell (born in 1726) who was the first breeder to carry out inbreeding. In sheep and cattle he was able to show that by matching related individuals with the properties desired and by discarding animals of other types in the offspring the goal set could be reached fairly rapidly. Soon, however, it was realized that inbreeding had also serious disadvantages in the shape of reduced vigor and fertility, and specific defects. In plant material Darwin's own experiments had taught him the striking difference in vigor between offspring after crossing and selfing.

Darwin states that degeneration from inbreeding can be checked, if the related individuals are separated during a few generations and exposed to different conditions of life. This may possibly be true, if the different conditions are such that a genotypic differentiation by recombination and selection will occur. It seems more likely, however, that the statement is just another expression of Darwin's belief that changed conditions mean changed properties owing to direct action of the environment, and that such changes will gradually become fixed and incorporated in the constitution.

Though Darwin had a thorough knowledge of the empirical results gained in inbreeding work, he was not able to give any plausible interpretation of these phenomena. In the twentieth century much work has been carried out to clarify the causes of degeneration from inbreeding and the favorable effects of outcrossing. Though several minor problems in this wide field of research certainly remain to be solved, the main features are now quite clear. We know that all cross-fertilizing higher plants and animals, including man, are heterozygous for numerous recessive genes, which very often are more or less deleterious when homozygous; and there is also evidence indicating that not only recessive genes, but also various alterations in chromosome structure, when homozygous, cause a reduction in vigor and fertility (*cf.* Müntzing, 1945; Bose, 1956, 1957, 1958). In *Drosophila* valuable methods have been elaborated for making various chromosomes homozygous and for testing the effects of such homozygosity (*cf.* Dobzhansky, 1957). The main result of these investigations is that almost every tested chromosome has been found to contain

several genes or "factors" which in the homozygous state cause more or less pronounced reductions in vigor or fertility. Thus, in *Drosophila* the chromosomes carry quite normally more or less clearly defined genes which in a homozygous condition are deleterious or quite lethal. In other organisms also a considerable amount of evidence has been obtained indicating that their gentoypes are also loaded with genes which cannot be homozygous without causing a depression in vigor or fertility.

Recent results in *Drosophila* and some other organisms (*cf.* Dobzhansky and Wallace, 1953; Dobzhansky and Levene, 1955; Lerner, 1954) demonstrate that heterozygosity does not mean only that deleterious genes are prevented from having unfavorable effects thanks to the presence of normal, dominant alleles. In addition to this, natural selection has led to the phenomenon called genetic homoeostasis, which implies that various combinations of gametes and chromosomes in the panmictic populations are adapted to each other and secure a maximum degree of vigor and stability against environmental disturbances. Thus, heterozygosity of this kind represents the normal condition, which will be upset by inbreeding, leading to increased degrees of homozygosity.

Present-day genetics explains not only why vigor and fertility are correlated with heterozygosity and homozygosity, but also why inbreeding leads to a morphological differentiation of the material. Shull (1911), working with maize, was the first one to observe how a naturally cross-fertilizing and fairly uniform population could by inbreeding be transformed into a series of distinct and constant, homozygous lines. We now know that this is simply due to the fact that the original population is not only heterozygous for genes influencing vigor and fertility but also for genes controlling a multitude of morphological characters. Homozygosity for these genes leads to an almost unlimited morphological polymorphism, each inbred line at the inbreeding minimum representing a distinct and uniform type. This corresponds to the "retention of character" which Darwin observed in inbred material of domestic animals, but for which phenomenon he was unable to give any plausible explanation.

IV. VARIATION OWING TO UNKNOWN INTERIOR CAUSES

Besides variation caused by environment, crosses, and inbreeding, Darwin was forced to admit the occurrence of peculiarities due to unknown laws, acting on the "organization" or constitution of the individual. In this connection he mentions that in man quite a catalogue of inherited malformations and predispositions to various diseases are known. He also refers to the occurrence of a quite specific finger defect, carried by both of two girl twins, and discusses in general the striking similarity often exhibited by twins. This in Darwin's view, demonstrates that the state of the parents at the exact period of conception, or the nature of the subsequent embryonic development, has a direct and powerful influence on the character of the offspring.

On the other hand, differences between brothers and sisters or between sister plants, derived from the same seed capsule and developed under closely similar conditions, are supposed to be caused by "unequal blending of the characters of the two parents and by the more or less complete recovery through reversion of ancestral characters on either side."

Cases of exceptional ineffectiveness of environment in causing and directing variation are also illustrated by several species and varieties, which have a wide distribution but nevertheless have essentially the same properties. In a host of other cases Darwin finds that variability could hardly be attributed to the definite action of the external conditions of life. Hence, he is led to attribute each slight variation much more to innate differences of constitution, however caused, than to the definite action of the surrounding conditions. This view was also supported by certain kinds of bud-variation, which, according to Darwin, must primarily depend on the constitution of the individual and only to a slight degree on the external conditions of life. Also the fact that beings produced sexually are much more liable to vary than those produced asexually pointed in the same direction.

It should be observed that in his analysis of the causes of biological variation Darwin met with several cases in which the characters of the parents were incapable of fusion and did not show the blending inheritance which he considered to be the general rule. From his descriptions it is evident that such characters were conditioned by single mutant genes in contrast to the polygenic and apparently blending inheritance of normal, quantitative characters. Thus, he states that some few characters are incapable of fusion but are unimportant, of semi-monstrous nature

and have been known to appear suddenly. In another connection he says that all characters which are transmitted in a perfect state to some of the offspring and not to others have been known to appear suddenly. The same view is expressed in the statement that man's attention has been struck by strongly marked modifications, which have suddenly arisen owing to some great disturbing cause in the organization.

Disturbing causes, such as crosses, may also induce other changes in the constitution, which often lead to reversions, the reappearance of characters derived from a more or less remote progenitor. According to Darwin reversion occurs so frequently that it is evidently an essential part of the principle of inheritance. Every character, which occasionally reappears, is present in latent form in each generation; and in every living creature a host of lost characters lie ready to be evoked under proper conditions.

According to Darwin's gemmule hypothesis variability ultimately depends on (1) deficiency, superabundance, fusion, and transposition of gemmules and on redevelopment of those which have long been dormant, (2) on the origin of new modified gemmules which finally, when sufficiently multiplied, will develop into new and changed structures. Each organic unit in a hybrid throws off hybridized gemmules but also dormant gemmules from both parents. When two hybrids pair there will be different possibilities for the combination of pure and hybridized gemmules.

According to the gemmule hypothesis each living creature is a microcosm containing gemmules, inconceivably minute and as numerous as the stars in heaven. Each plant and animal is also compared to a bed of mould full of seeds, most of which soon germinate, some lying dormant for a period while others perish. Evidence that the gemmules are thoroughly diffused is, according to Darwin, represented by the fact that in certain plants complete new individuals may be regenerated from a minute fragment of a leaf.

COMMENTS

From some of the observations described above it is clear that Darwin had repeatedly seen or heard of effects caused by single mutant genes. To this category belong the cases on non-blending inheritance of strongly marked "modifications," which Darwin considered to have arisen from some great disturbing cause in the organization. Further examples of the same kind are represented by the bud variations and the long catalogue of inherited malformations in man. Such cases could not be convincingly accounted for by the gemmule hypothesis, and, though ingenious, we now know that this hypothesis is almost entirely wrong. The hereditary constitution is not an extract of the body cells, and variability is not caused by quantitative changes and fusion of already existing or newly formed gemmules, or by redevelopment of dormant gemmules. It must be admitted, however, that in some respects the gemmules are similar to genes. They were supposed to be extremely small and numerous, and variation in their number would affect the morphological characters. In hybrids different combinations of gemmules were supposed to occur, giving rise to variability in the offspring. A fundamental difference is that Darwin believed that a hybrid forms hybridized gemmules, whereas Mendel discovered that hybrids form pure gametes, containing only one member of an allelic pair of genes.

Darwin's discussion of the twin pair, in which each member had the same specific finger defect, led to the somewhat frightening conclusion that the state of the parents at the exact period of conception or the nature of the subsequent embryonic development has a direct and powerful influence on the character of the offspring. Fortunately we now realize that such cases are present in identical twins simply because they have got exactly the same genotypical constitution.

It is interesting to see how Darwin's great belief in the profound ability of variable conditions of life to cause inherited biological variation is markedly shattered by observations such as those just discussed. He is forced to admit that the organisms have an important interior constitution, which is not only an image of the exterior properties, but also obeys mysterious and unknown laws, which he did not succeed in solving.

V. EFFECTS OF SELECTION

1. DIFFERENT KINDS OF SELECTION AND THEIR INTERACTION

Darwin regards prevention of free crossing and the intentional matching of individual animals as the cornerstones of the breeder's art. This procedure involves intentional or methodical selection, which is now practiced after a long period of unconscious selection. By this term Darwin means the preservation by man of the most

valued individuals, and the destruction of the least valued ones without any conscious intention on his part of altering the breed. Unconscious selection is extremely old and has certainly been carried out ever since domestic animals and cultivated plants were taken into the service of man. As Darwin points out, when primitive races suffered from famine, they certainly slaughtered the less useful animals and only saved the very best ones. With plants, from the very dawn of civilization, the best variety known at each period would generally have been cultivated and its seeds sown. Thus, says Darwin, there will have been some selection from an extremely remote period and among the most barbarous nations, but without any prefixed standard of excellence or thought for the future.

There are quite continuous transitions between unconscious and methodical selection and, as Darwin says, the individual frame of mind of a breeder will influence the characters of his stock without any conscious intention of forming a new deviating type. Natural selection has also played an important part in the origin of our domestic animals and cultivated plants. A simple example of this kind is winter hardiness in cultivated plants, such as wheat. If the starting material is heterogeneous, only types with a minimum degree of hardiness will survive in a certain region. Natural selection sometimes favors but often checks man's power of selection, especially when the methodical selection tends to go to unnatural extremes.

Darwin considered unconscious selection to have produced much more important results than methodical selection, which has been practiced during a much shorter time. Though the methodical selection involved in modern plant and animal breeding has very markedly increased the value of our cultivated plants and domestic animals, we can agree with Darwin that the excellent products we now see everywhere have been obtained through the joint and successful action of natural, unconscious, and methodical selection. We can also agree that wherever selection is not practiced, distinct races are not formed.

Darwin gives an excellent historical survey demonstrating that selection was already performed in ancient times; he also informs us convincingly that selection is carried out to a surprisingly high and efficient degree even by semi-civilized people. All imaginable characters have been subject to selection and in most cases with a more or less positive result.

2. SELECTION WITHIN A RACE AND SELECTION AFTER CROSSING

The possibility of selection rests on variability, and Darwin clearly shows that spontaneous variability is present in almost every population. In a herd of sheep the different individuals are very similar, but so-called sheep-classifiers are able to distinguish very slight differences, which are of importance for breeding work. In a herd of reindeer the Laplanders are said to be able to recognize the individual; and by special experiments Darwin obtained evidence that ants are individually distinct and recognize each other.

He stresses that selection requires a keen eye and considerable endurance, and that even the breeding of, for instance, fancy pigeons is no simple art. Such selection work is based on scarcely appreciable differences, which may very slowly be accumulated to a clearly visible result.

Selection within a race may sometimes only be aimed at keeping the material reasonably pure; and a simple method with this end in view is seed-bed roguing, by which clearly deviating individuals are removed already at the seedling stage. Darwin was aware that all highly improved races, if neglected or not subject to incessant selection, soon degenerate as a consequence of continued variability and reversion.

The possibilities of selection are evidently much increased by crossing, and Darwin states that crossing with the aid of rigorous selection during several generations has been a potent means of modifying old races and of forming new ones. Various good examples of this kind from pigs, sheep, cattle, and chickens are given, and Darwin also refers to similar results obtained in turnips and wheat. In these cases crosses have either been undertaken once only for the sake of modifying some particular character, or in other cases, as with the development of the present races of cattle, pigs, sheep, and chickens, repeated crosses have been performed. In all cases selection has been intensive and has led to remarkable results. After a thorough discussion of the large amount of data available, Darwin concludes that selection is the paramount power in the formation of domestic breeds and also the leading force in the formation of new species.

3. DIVERSITY OF SPECIAL PARTS OF AN ORGANISM

The strong effects of selection are also well illustrated by the fact that in various kinds of domestic animals and cultivated plants the greatest

amount of variability is always exhibited by that part of the organism which is of the greatest practical importance and value to man.

Thus, for instance, Darwin points out that the varieties of cabbage and kale differ very much in their foliage and stems, which are the selected parts, and closely resemble each other in their flowers, capsules, and seeds, which have not been subject to selection. With animals we see something of the same kind, says Darwin. Sheep are valued for their wool, and the wool differs much more in several races than the hair in cattle. Neither sheep, goats, European cattle, nor pigs are valued for their fleetness or strength; nor do we possess breeds differing in these respects like the race horse and dray horse. Dogs are valued for their mental qualities and sense, and everyone knows how greatly the races differ in those respects. On the other hand, where the dog is valued solely for the purposes of food, as in the Polynesian islands and China, it is described as an extremely stupid animal.

Darwin also points out that in most organisms methodical selection would be able to induce a strong variability also in other characters which are now of no particular interest from a practical point of view. Thus, as a rule, all imaginable characters show some degree of variation, and if this variation is affected by a strong selection, the result will almost always be very marked deviations and a strong polymorphism.

4. COMMENTS

Darwin's views on the importance of different kinds of selection for the origin of improved types of domestic animals and cultivated plants are still quite correct. Modern genetics has amply confirmed that as long as a biological material is genetically heterogeneous, selection with the help of mutation and recombination may lead to surprisingly great changes. In recent years this has been tested and verified by several workers studying, for instance, the effects of plus and minus selections for bristle numbers in *Drosophila*. It is true that within a pure line of a homozygous self-fertilizing plant, such as the bean material studied by Johannsen (1903, 1909), selection is not able to change the type, but in crossfertilizing species, such as those studied by Darwin, recombination always furnishes material on which selection may work.

In two respects our views on selection today differ from those of Darwin. As we know that environmental variations are not inherited, a still stronger emphasis is placed on selection as a means of changing a biological material in a certain direction. On the other hand, we also know that genetic polymorphism is not always and entirely the result of selection. In small populations random distribution of genes, genetic drift, may also occur.

At any rate we can fully agree with Darwin that selection—methodical, unconscious, and natural—is of the utmost importance not only for the development of our domestic species but for species formation and evolution in general.

VI. DARWIN'S VIEWS ON THE ORIGIN AND DEVELOPMENT OF DOMESTIC ANIMALS

As we have already seen from the previous chapters, Darwin concludes that domestic animals and cultivated plants have arisen by a combination of variation and selection. This is also clear from the following quotation:

> Species after having retained the same character for countless ages when domesticated have varied in the most diversified manner, that is, have failed to transmit their original form. Man does not attempt to cause variability, though he unintentionally affects this by exposing organisms to new conditions of life and by crossing breeds already formed. The possibility of selection rests on variability and this mainly depends on changed conditions of life, but is governed by infinitely complex and to a great extent unknown laws.

From this it is clear that, in the first place, Darwin ascribes variability in domestic species to changed conditions of life and secondarily to crosses between already existing breeds. Thirdly, selection by man still more increases variability and leads to more or less distinct races. This process is described by Darwin in the following way:

> As there is no limit to man's desire to possess animals and plants more and more useful in any respect, and as the fancier always wishes, from fashion running into extremes, to produce each character more and more strongly pronounced, there is a constant tendency in every breed, through the prolonged action of methodical and unconscious selection, to become more and more different from its parent-stock; and when several breeds have been produced and are valued for different qualities, to differ more and more from each other. This leads to Divergence of Character. As improved sub-varieties and races are slowly formed, the older and less improved breeds are neglected and

decrease in number. When few individuals of any breed exist within the same locality, close interbreeding, by lessening their vigour and fertility, aids in their final extinction. Thus the intermediate links are lost, and breeds which have already diverged gain Distinctness of Character.

Consequently, according to Darwin, the degree of distinction between various domestic breeds depends on the amount of "modification" they have undergone and especially on extinction of the linking, intermediate, and less valued forms.

The present distinctness between various domestic races has erroneously led the breeders to believe, says Darwin, that all the chief breeds are aboriginal productions, but this view is just as incorrect as that held by many systematic naturalists, who believe that closely allied natural species may not have descended from a common progenitor.

Though some domestic animals probably have a monophyletic origin others (e.g., dogs, cattle, pigs) are considered by Darwin to have descended from more than one species or wild race. In such cases crossing came into play at an early period and was an aid in the formation of our present races. It is not likely, says Darwin, that semi-civilized men would have taken the necessary pains to modify by selection their commingled, crossed, and fluctuating stock. Nevertheless, this material must have been stabilized by natural selection, later followed by unconscious and methodical selection.

With regard to cultivated plants, Darwin thinks that the great improvement of all our anciently cultivated plants, just as in animals, may be attributed to selection long carried on, in part methodically and in part unconsciously. His examples in support of this statement are chiefly drawn from ornamental flowers, but he also mentions that by selection over a long period of years the early maturity of peas has been hastened by from ten to twenty-one days. He also mentions the beet plant, which since its cultivation in France, has almost exactly doubled its yield of sugar as a consequence of careful selection.

Sometimes the distance between wild progenitor and cultivated plant seems to be quite short. Darwin informs us that a certain Mr. Buckman, by culture and careful selection, converted parsnips, raised from wild seed, into a new and good variety. Many of the ornamental plants are of relatively recent origin and none of them older than from the sixteenth century. At any rate, according to Darwin, the earliest known flower-garden in Europe, namely at Padua, dates only from the year 1545.

That great improvements have also been obtained in the ancient and more important cultivated plants is demonstrated by comparisons between preserved seed material from ancient times and seeds of our present varieties. Thus, in wheat, barley, oats, peas, beans, lentils, and poppy the grains and seeds from the varieties cultivated in Switzerland during the Neolithic and Bronze periods were much smaller than the seeds of present varieties. Therefore, Darwin does not hesitate to conclude that also among cultivated plants "we at the present day profit by a course of selection occasionally carried on during thousands of years."

In animals selection has, on an average, also resulted in larger breeds. According to Darwin, Rütimeyer has shown that the sheep and cattle which were kept by the earlier lake inhabitants in Switzerland were smaller than our present breeds, and archaeological findings from Denmark reveal a similar development not only for sheep but also for dogs and horses.

Though Darwin stresses the enormous importance of unconscious selection carried out during thousands of years, he also gives some very striking examples of what methodical selection may accomplish in relatively short periods. In the days of Darwin very intensive work of this kind was carried out in England, as is evident from the following quotation:

> What methodical selection has effected for our animals is sufficiently proved, as already remarked, by our Exhibitions. So greatly were the sheep belonging to some of the earlier breeders, such as Bakewell and Lord Western, changed, that many persons could not be persuaded that they had not been crossed. Our pigs, as Mr. Corringham remarks, during the last twenty years have undergone, through rigorous selection together with crossing, a complete metamorphosis. The first exhibition for poultry was held in the Zoological Gardens in 1845; and the improvement effected since that time has been great.

A feature in domestication which deserves special attention is the retainment of fertility under new and changed conditions. In most cases the fertility of the wild progenitors is not only retained but also increased. Domestic animals breed more often in the year and produce more young at a birth than wild animals of the same species; they also sometimes breed at an earlier

age. Darwin attributes this difference to the more abundant supply of food enjoyed by domestic stocks.

According to Darwin excess of food and other unnatural conditions may, however, in some cases give rise to an opposite effect. As already mentioned above (p. 192), this is the explanation he is inclined to give for the sterility occurring in many highly cultivated plants, such as pears, pineapples, bananas, and sugar cane.

Of still more interest than the usually increased fertility in domestic species is the absence of barriers to crossability, which is characteristic of domestic varieties of animals as well as plants. In spite of the enormous differences in size and other respects all races of dogs are completely interfertile, and the same thing is met with in other domestic species. Darwin repeatedly refers to this so-called Pallasian doctrine, which says that species after having been domesticated lose their natural tendency to sterility when crossed. The striking thing is that natural species, sometimes distinguished by quite small morphological differences, are intersterile, whereas domestic races, which may widely differ, nevertheless intercross without difficulty and give fertile hybrids. This occurs also in domestic species (dog, cattle, pig), which are supposed to be derived from more than one aboriginal species or race.

Though newer investigations tend to show that the descent of these animals may be less polyphyletic than Darwin believed (*cf.* below p. 208), the interfertility between widely different races of dogs and similar cases in other domestic species really represent a problem which may not yet be entirely solved. It is not excluded that by the intercrossing involved in domestication, genetically balanced and adjusted barriers of sterility, which occur between natural species, may have been broken up. This may possibly be compared to the fact that mechanisms of self-incompatibility in higher plants may break down in various ways as a result of mutation, inbreeding, or chromosome doubling (*cf.* Lewis, 1954; Lundqvist, 1958). Species crosses may also weaken the self-incompatibility mechanism (*cf.* Mather, 1943).

COMMENTS

The only criticism which can be directed against Darwin's views on the origin and development of domestic species concerns his conviction that variability, on which the possibility of selection rests, mainly depends on changed conditions of life, though governed by complex and unknown laws. Otherwise, his argumentation is essentially correct, and his observations and conclusions are, indeed, of fundamental importance for all later investigations in this field of research.

Since Darwin's time, however, a large number of new facts have accumulated, and new ways of forming domestic species have been discovered, which were entirely unknown to Darwin. This requires special chapters in which we shall distinguish between the development of domestic animals and the formation of cultivated plants.

VII. SOME NEW DATA CONCERNING THE ORIGIN AND DEVELOPMENT OF DOMESTIC ANIMALS

Though a quantity of new data has accumulated since Darwin's time, nothing essentially new, regarding the origin of domestic animals from wild species and their improvement by selection, has really developed. The most interesting data have been obtained from the breeding of some young domestic animals, in which it has been possible to follow from the outset their behavior under domestication. As such cases also tend to elucidate the origin and properties of older domestic species we shall start with some data concerning the development of the domestic rabbit and the recent breeding work with various fur animals.

1. THE DOMESTIC RABBIT

As pointed out by Nachtsheim in his valuable book *Vom Wildtier zum Haustier* (1949) the development of the domestic rabbit may serve as an excellent model for similar processes in other domestic animals.

The domestic rabbit is derived from wild rabbits, imported from Spain during the Roman Empire and brought into so-called leporaries, closed-in and fenced areas, at first used only for hares. Here the animals lived as in the wild but could not escape, thus being easily accessible for hunting parties. Old engravings show that rabbit hunts in leporaries were considered to be a pleasant and undangerous pastime for fair ladies.

In contrast to the hares the rabbits were able to breed in the leporaries without difficulty. The next important step in their domestication was that monasteries in France started rabbit breeding, keeping the animals in their yards in such a way that they were prevented from building subterranean burrows. In this way man for the

first time got the opportunity to follow and study rabbits during their whole life cycle.

A document of the year 1149 shows that rabbits had then been introduced into Germany, but not until the seventeenth century is there any evidence of an incipient differentiation into different races. The very first step in the domestication, here as in other animals, must have been a psychological change by mutation from wildness and shyness to tameness. At the end of the seventeenth century this stage had been reached and the rabbit had also been changed in other respects. In medieval times the rabbit was exclusively or primarily bred for meat, but in the sixteenth and seventeenth centuries the fur coat of the rabbit gained more and more importance and at the end of this period at least seven mutant types with colors different from the wild type were known. Nachtsheim, on the basis of recent profound knowledge of the genetics of the rabbit, is able to specify the gene formulae for these seven types.

In the period 1700 to 1850 development was slow, but two new genes for coat color and the gene causing Angora hair were added. After 1850, and especially after 1900, the differentiation into races has become more and more rapid. After Mendel's principle of recombination of genes had become known, new races were not only based on occasional new mutations (in this century six additional ones for hair-coat characters) but to an increasing degree on crossing and selection of new combinations of genes. At present more than 50 well-established breeds of the domestic rabbit are known, but enormous possibilities of producing new types by recombination still remain to be utilized.

2. NEW DOMESTIC FUR-PRODUCING ANIMALS

According to Venge (1953), the modern breeding work with fur animals was started in Canada in 1879, the first material being silver foxes. Until 1910 this breeding work was monopolized but was afterwards taken up also in other countries. Work with blue foxes was also started in America a few years later than silver-fox breeding. Breeding work with the mink is probably more recent, but it is uncertain where and when the first trials were made. In the 1930's there was a very marked increase in mink breeding. Other fur animals also have recently been more or less domesticated. However, in the present connection we may limit ourselves to some data from fox and mink breeding.

A. Fox Breeding

The start of this breeding was conditioned by the appearance of two different kinds of foxes (Alaska black fox and Standard black fox), representing mutations in two different loci of the red fox. Gene formulae: red fox $A_1A_1A_2A_2$; Alaska black fox $A_1A_1a_2a_2$; standard black fox $a_1a_1A_2A_2$. Backcrosses to the red fox gave two additional, distinguishable heterozygous types with the formulae A_2a_2 and A_1a_1, respectively.

The next type, the silver fox, is a lighter variant of the black fox and is conditioned by multiple genes. It has arisen by selection, and there are different gradations of silver hairiness.

The so-called platinum fox, having an ash-blond coat with a dark stripe on the back, is conditioned by a mutation in the gene for full pigmentation. It arose in Norway in 1933 and a few years later three new cases of mutation, probably at the same locus, were met with. The platinum gene is dominant and lethal in double dose. The same is true of the mutant gene for white face, which arose in Canada in 1928. Other cases of white-face mutations have been described, which are not all identical but have partly additive effects.

Golden platinum foxes are heterozygous in the A_1 gene and the platinum gene and are obtained from crosses between so-called bastard foxes ($A_1a_1A_2A_2$) and platinum foxes. Pearl foxes are conditioned by two different recessive mutants of the standard silver fox. Without giving further details it may be mentioned that a series of other fox types (perlatina, glacier blue, Washington platina, radium fox and pastel fox) have recently arisen and are conditioned either by new mutant genes or combinations of two genes. The genes for complete pigmentation, white face, and platinum form a series of multiple alleles, which are all dominant over albino.

B. Mink Breeding

The mink (*Mustela vison*) is native in North America and is represented there by thirteen local races. Three of these races (the Alaska, Kenai and Eastern types) have been of importance for the domesticated types, probably with some intermixture of four other local races. None of these races differ essentially from each other and nowadays, from a practical point of view, the coat color is a more adequate basis of subdivision. Thus, besides the standard mink there are not less than fourteen other types which differ from

the standard type in one single gene. Of these mutant types nine are recessive and five dominant to the standard type. One of the dominant genes is known to be lethal when homozygous. Three of the genes form a group of multiple alleles, and at least one case of linkage has been detected. The polymorphism of the present mink material is not only caused by single mutant genes but also by certain combinations of genes. A much larger polymorphism will certainly be eventually obtained by recombination as well as by new cases of mutation.

C. Conclusions

The evidence from fox and mink breeding strikingly shows how the wild type or standard type relatively soon gives rise to deviating types, which may be taken care of and preserved by the breeders. At least the dominant genes must have arisen by mutation, occurring among the domesticated animals. The recessive genes, which suddenly appear, may have been present in the original population, but just as in *Drosophila* or *Zea mays* all these recessive types deviate clearly in single genes. It is therefore of no particular consequence whether the recessive alleles have arisen by mutation in the wild state or not until domestication has begun.

Just as in the domestic rabbit a limited degree of polymorphism is caused by the appearance of each separate mutant type. A much greater polymorphism will result from recombination of the different genes. Finally, it should be observed that in the fox and mink, just as in the rabbit, some genes are more or less deleterious or quite lethal in double dose. In a wild state natural selection would tend to eliminate such genes.

3. DOMESTICATION CHARACTERS

There can be no doubt that the psychological difference between wild and domesticated animals has arisen during the period of domestication by the combined action of mutation, recombination and selection. In the rabbit, where we can survey the whole history of domestication, there is no doubt that our present docile races are descendants of animals which certainly have been just as wild as the wild rabbits now living. Comparative anatomical investigations of wild type and domestic types of rabbits as well as of some other animals (*cf.* Nachtsheim, 1949; Herre, 1955) have revealed that the brain is larger and the senses sharper in the wild animals than in their domesticated relatives. This may be the result of a long period of selection, and Johansson (1953*b*) believes that in the swine the troublesome ferocity of the wild progenitors has been gradually eliminated by selection. Sometimes this transformation seems to be easy. Johansson (1953*a*: 13) mentions that although silver foxes have only been under domestication during some thirty generations, individuals are not rare which show the same affection to their masters as a dog. Thus, the step from the wild to the domesticated state is sometimes not very large. Høie (1953) reports that in the domesticated goose, which has undergone a very long period of domestication, it may nevertheless happen that individual wild geese may join flocks of domesticated geese and remain with them permanently. Other animals like the reindeer are half-domesticated, living a comparatively free life but being under the influence of man.

In other cases domestic animals are like living machines with a one-sided, highly developed production. Such domestic breeds, which are the result of human selection, are also entirely dependent on man for their existence. High-bred leghorn chickens, for instance, can only be propagated with the help of incubators as this race almost entirely lacks the instinct of sitting on the eggs. The productivity of such races is exceedingly high compared to their wild relatives. According to Johansson (1953*a*: 38) leghorn hens during a period of 500 days produced on an average 181 eggs, whereas nonbred bankiva hens only gave 63 eggs during the same period and under the same conditions.

The higher productivity as well as all other domestic characters are certainly in part environmental modifications, resulting, for instance, from the increased amount of food given to the animals. To a still higher degree the domestic characters are certainly the result of a changed genotypical constitution. Often the characters induced are not only one-sided and driven to extremes but are also correlated with obvious disharmonies (*cf.* Herre, 1955: 821) or pathologic alterations. A classical case is the shortlegged Dexter type in cattle, in which the gene causing the short legs is lethal when homozygous. A relatively mild pathological alteration is represented by the rex rabbit, the physiological inferiority of which was discussed above (p. 194). Nachtsheim (1949: 98–107) gives a series of other similar examples and also mentions that in the domestic rabbit

some twenty different hereditary anomalies and diseases are known, which affect all organs of the animal.

A striking feature in many domestic animals is the strong variability in size between various races, the contrast between giants and dwarfs sometimes being very pronounced as in dogs, horses, and rabbits. There is some evidence (*cf.* Herre, 1936; 1955) that such differences may be caused by deviations in the endocrinic system, and Johansson (1953*b*: 347) believes that in domesticated swine there are still great possibilities to change the endocrinic type and in that way body structures and speed of development in the direction desired.

4. MONO- OR POLYPHYLETIC ORIGIN OF DOMESTIC ANIMALS?

The first domestic animal, the dog, can be traced to about 10,000 years B.C. and other archaeological findings indicate that in about 8000 B.C. there were at least two races of this animal. Other domestic animals make their appearance on the scene some time between 6000 and 2000 years B.C. The longer the time of domestication, the more difficult it is to get reliable information concerning the wild progenitors. The oldest domestic animals are supposed to have had a polyphyletic origin, whereas with regard to all younger ones there is more or less conclusive evidence that they are monophyletic. Under such circumstances the suspicion arises that the oldest domestic animals may also have a monophyletic origin.

Darwin believes that cattle, pigs, and dogs are almost certainly the descendants of more than one wild "form." With regard to cattle he regards the Indian cattle, the zebus, to be specifically distinct from our own cattle and further regards the European cattle as descendants of three different forms or species of *Bos*. Nowadays (*cf.* Korkman, 1953) zebu and European cattle are included in the same species, as they are perfectly interfertile. It is also generally considered that European cattle as well as the zebu cattle are both descendants of the aurochs, *Bos primigenius*. It is generally believed that domestic cattle were first produced in Mesopotamia in the period 5000 to 4000 B.C. In Egypt there have been high-bred cattle since 4000 to 3000 B.C. In cattle, as well as in other species, there is reason to believe that domestication occurred on several occasions and at different places. This would result in racial differentiation from the beginning, and from these starting points new races may have been formed later by mutation, crossing, recombination, and selection.

With regard to pigs the wild boars of Europe and Asia are not regarded as belonging to different species any more, but only as subgroups of the same species, *Sus scrofa*. Both these racial groups have contributed to the formation of our modern, high-bred races. Several different centers of domestication have been distinguished.

Darwin concludes that the domesticated dog has descended from two good species of wolf (viz. *Canis lupus* and *C. latrans*) and from two or three other doubtful species of wolves; from at least one or two South American canine species; from several races or species of the jackal and perhaps from one or more extinct species. Foxes also have been supposed to be included in the ancestry of dogs, but this is excluded for several reasons, especially because it is impossible to hybridize the two species. Though the origin may not be strictly monophyletic, it is nowadays generally assumed that the dog is less polyphyletic than Darwin thought. It should be noted, however, that dogs give fertile hybrids not only with wolves but also with jackals (*cf.* Klatt, 1927). It is also a fact that the wolf is a very polymorphic species, which is split up into several subspecies and geographic races. Even if the dog is chiefly descended from the wolf, the polymorphism in the original species and the occurrence of repeated cases of domestication will tend to give rise to several different primary types of dogs. Crosses between these and occasional backcrosses to the wolf will further increase the polymorphism; and to a minor extent crosses with jackals may also have contributed to the variability. Certainly, mutations have also occurred, and under all these circumstances we can fairly well understand why the dog shows such extreme ranges of variation, and why the different breeds are nevertheless interfertile. It should be pointed out, however, that an equally strong polymorphism is met with in the domestic pigeon, though recent workers agree with Darwin that all these races are descended from only one wild progenitor, the rock pigeon, *Columba livia*.

In several cases it is a matter of taste, whether a domestic species should be considered to have a mono- or polyphyletic origin. Such is the case with the sheep, the wild progenitors of which are supposed to be three "species," which are interfertile with each other (*cf.* Nachtsheim, 1949).

Berge (1953) points out that during long periods there has been no sharp line of demarcation between wild and domestic sheep and that the wild types which may be considered as progenitors are closely related. According to Berge, it is most reasonable to assume a monophyletic descent from forms similar to the urial (*Ovis vignei*). A similar situation is met with in goats, which are probably in the main descended from the bezoar goat (*Capra aegagrus*) though other closely related and interfertile races or "species" may also be involved (*cf.* Nachtsheim, 1949; Berge, 1953).

Domesticated ducks are supposed to be derived chiefly from *Anas boscas* (*cf.* Høie, 1953: 479), but other closely related species may also have contributed (*cf.* Hagedoorn, 1939: 282). With regard to the domestic fowl Darwin considered them to be derived from one single species, *Gallus bankiva*. Some later authors believe that other wild species of *Gallus* may also be involved but the question is not settled (*cf.* Høie, 1953: 430).

VIII. SOME NEW DATA CONCERNING THE ORIGIN AND DEVELOPMENT OF CULTIVATED PLANTS

1. AGE

Cultivated plants are of very different age, the oldest ones being as old as our present culture and civilization, the youngest ones being quite recently adopted by man. The plants first cultivated were certainly species which had been found to be useful already in the wild state, producing seeds, berries, tubers or other parts suitable for food. A typical plant of this kind is the raspberry, of which the garden forms are fairly recent. Still younger is *Hippophae rhamnoides*, previously utilized in the wild state, but now brought into culture in Germany on account of the high concentration of vitamin C and karotin in the fruits (Schwanitz, 1957).

Agriculture began when man started to cultivate plants, previously found to be useful in the wild, and this is considered to have happened about 7000 years ago. About 4000 B.C., agriculture was already well developed in Egypt, barley, emmer wheat and some leguminose plants being the most important crops. The einkorn wheat, *Triticum monococcum*, is also very ancient in Europe as well as in Asia minor. Mangelsdorf (1957) has reported that carbonized kernels of wheat were found recently at the 6,700-year-old site of Jarmo in eastern Iraq, the oldest village yet discovered, a village which may have been one of the birthplaces of man's agriculture. There were two types of kernels in the Jarmo site, one corresponding to cultivated *T. monococcum*, and the other to the wild related species, *T. aegilopoides*, still growing wild in the Near East.

Bread wheats are evidently younger than einkorn and emmer wheat and can be traced back to about 2500 B.C. (For details concerning the origin and distribution of the wheat species, *cf.* Schiemann, 1932; 1943.)

Among the cereals, rye and oats are younger than wheat, the first archaeological findings in Europe of both species being from the Bronze Age (about 2000 to 1000 B.C.). The primary center of origin of maize is probably the Andes of Bolivia and Peru where already in prehistorical times it was an important cultivated plant. The Asiatic rice and soya-beans have also been in culture for a very long time, their age being at least 4,500 years.

The potato, *Solanum tuberosum*, was not brought to Europe until the end of the sixteenth century and once more in the nineteenth century, the great polymorphism of our present cultivated potatoes thus being derived from a rather limited number of primitive forms. Beets and mangels of different kinds are known since about the sixth century B.C., but it was not until 1747 that saccharose was detected in beet roots. In the nineteenth century real sugar beets were evolved from mangels by long-continued and intensive selection and, consequently, this important sugar producer is of relatively very recent origin. Of still more recent origin as cultivated plants are some forest trees, and of these the most important ones are still more or less in the wild state.

From the examples given we learn that the array of cultivated plant species is not given once and for all but, on the contrary, new species are continuously found to be useful and are brought into culture. On the other hand, some species which were formerly widely cultivated are now on the verge of extinction, or have quite lost their role as cultivated plants but possibly to some extent living on as weeds (*cf.* Schwanitz, 1957: 131).

2. ORIGIN AND POLYMORPHISM

As indicated above, and as already realized by Darwin, the cultivated plant species have gradually evolved from wild relatives, and for the ma-

jority of them these wild relatives can be indicated with certainty. With regard to their mode of origin it is useful to distinguish between *primary* and *secondary* cultivated plants.

The primary cultivated plants have been directly brought into culture on account of various valuable properties. Ecologically they are characterized by being ruderal plants, preferably living at dumping grounds with a soil very rich in nutrients. To this group belong, for instance, most wheat species, barley, rice, maize, sugar cane, tobacco, flax, soya, rape, and cotton.

The secondary cultivated plants are younger and decidedly anthropochorous because their need of nitrogen and other nutrients is best satisfied close to human settlements. To this group belong, for instance, hemp, poppy, kale and cabbage, mangels and beets, and different medicinal plants.

An especially interesting group of secondary cultivated plants consists of those which, before being brought into culture, occur as weeds in the fields of primary cultivated plants. A classical case of this kind is represented by rye, which in its center of origin in Asia Minor may occur as a weed in fields of wheat. At higher altitudes, where the better frost hardiness of rye than of wheat becomes important, the former may gradually replace wheat and finally dominate completely (*cf.* Schiemann, 1932: 179). Thus, in these cases the altitude will decide whether the rye is to be regarded as a weed or as a real and cultivated cereal. In the development of cultivated rye a change from a primitive stage with brittle rachis to a more advanced stage with tough rachis has also been of great importance, and the same is true of a change from perennial to annual habit of life.

As may be seen very beautifully, especially in the weeds occurring in cultures of flax, selection has allowed such strains to survive which with regard to seed size and in other respects are as similar as possible to the host plant. The degree of similarity has even been found to be proportional to the degree of selection. By this peculiar mechanism some of the linseed weeds have developed into really useful cultivated plants such as species of *Camelina, Spergula, Sinapis, Eruca,* and *Brassica* (*cf.* Schwanitz, 1957: 100–107). Other still more important secondary cultivated plants have also arisen as weeds, but in cultures other than linseed. This is, for instance, true of different species of oats, peas, beans, etc. Interesting enough, new types of cultivated plants begin to appear as weeds in secondary cultivated plants. Thus, according to Schwanitz, there are in rye some species of *Bromus, Agrostemma,* and *Avena,* which are promising in this respect, and in oats certain varieties of *Avena strigosa* occur as weeds but have been found to be useful in pure cultures on certain poor soils in Northwestern Europe. It should be remembered that ordinary oats itself (*Avena fatua* ssp. *sativa*) has developed from *Avena fatua* ssp. *fatua,* which is a weed in emmer wheat and barley.

Already de Candolle (1855, 1883), and later on especially Vavilov (*cf. Selected Writings of N. I. Vavilov,* 1951), detected and explored so-called *centers of origin* of cultivated plants. More correctly, these centers represent areas in which a particular species shows a maximum degree of polymorphism and where, consequently, the supply of genes for various characters is especially rich. According to Vavilov, dominant genes are especially frequent in such areas but are gradually replaced by the corresponding recessive alleles in more peripheral regions. Vavilov regarded the centers of greatest polymorphism also as the real center of origin of the plant in question.

This view has been criticized (*cf.* Schiemann, 1932; Schwanitz, 1957), and it has been realized that some of these centers may be secondary centers in which a migrating species may have found especially favorable conditions. The eight centers in question are all mountain areas in tropical or subtropical parts of the world. Already the edaphic structure with separating mountain ridges and deep valleys will favor polymorphism, and this is further supported by a primitive agriculture, each peasant securing his own seed material. Wide variations in temperature will tend to induce mutations, and new mutant types will have good chances of finding suitable ecological areas where they may exist and develop. Thus, though it must be somewhat uncertain whether the centers of the greatest diversity are also the centers of origin, the exploration of such centers is certainly of the greatest importance to agriculture, especially as valuable genes present in such areas may be utilized in future plant-breeding work. Already genes for disease resistance and other valuable properties are being drawn from primitive varieties or wild species.

3. MECHANISMS OF DEVELOPMENT. SOME PLANT-BREEDING METHODS

A. Selection in Genotypically Variable, Cross-fertilizing Plants

Concerning the mechanisms of development of cultivated plants it is still largely true, as Darwin concluded, that cultivated plants, just as domestic animals, are developed by natural, unconscious and methodical selection, operating on their inherent tendency to variation.

In most cultivated plants with an unchanged chromosome number selection has simply utilized the spontaneous variation in the material, which, as we now know, is directly due to the heterozygosity characteristic of cross-fertilizing plants. This heterozygosity must ultimately be due to spontaneous mutations, more or less slowly accumulated in the material, and the practically important characters are in such cases conditioned by multiple genes.

The history of our varieties of kale and cabbage is fairly well known and goes back to the younger Neolithic period. The improvements have occurred at long intervals, one valuable mutant gene being added to another. By genetic analysis of our present varieties it has been found that head formation in cabbage as well as the crisping of the leaves in green kale is due to three genes in each case (*cf.* Schwanitz, 1957). In the cereals the practically important toughness of the rachis of the ear is conditioned by two or three genes. In a similar way we may assume that improvements have also occurred in other cultivated plants, though as a rule the number of genes involved in each case is not known and is probably often quite high.

A good example of what selection can accomplish is represented by the origin of the sugar beet in the nineteenth century (*cf.* above p. 209). In the beginning of the century Achard started to produce sugar beets from mangels, and in about one hundred years of intensive selection the sugar percentage in the roots has been increased from about 7 per cent to more than 20 per cent. At the same time the sugar beet has been improved in other ways and is now certainly a specific and highly important cultivated plant.

B. Breeding by Crossing and Recombination

Related to the previous category are those cases in which the spontaneous variation by recombination (which is quite absent in homozygous self-fertilizers like wheat and barley) is much increased by crosses. Already Darwin knew, as we have seen (p. 197), that crosses tend to increase variability in the offspring of the primary hybrids. As early as the previous century crossing was sometimes used to increase the possibilities of selection. When Mendel's laws of inheritance had been rediscovered in 1900, it was soon realized that his principle of recombination could be utilized in plant-breeding work. The classical paper in this field was written by Nilsson-Ehle (1906), who emphasizes that crosses should not be undertaken merely in order to increase the general variability of the material but, on the contrary, with a clear plan to combine valuable properties of both parents into one new variety. He also gave examples which demonstrated that such recombination is possible, though it is complicated by the fact that numerous genes are generally involved in quantitative characters of practical importance (Nilsson-Ehle, 1909, 1911).

It is also well known that such breeding by crossing and recombination has led to products of great economical importance not only in Sweden but in all other countries where this method has been tried. It is still one of the most important methods in modern plant breeding.

C. Utilization of Spontaneous Mutations

The importance of spontaneous mutations in plant-breeding work is particularly well illustrated by the recent development of *sweet lupines* by v. Sengbusch and collaborators (*cf.* v. Sengbusch and Zimmermann, 1947). As Schwanitz (1957) points out, this represents a case in which during the last thirty years we have seen a new cultivated plant species arise before our eyes.

The starting material consisted of the three wild species *Lupinus albus, L. luteus,* and *L. augustifolius,* which may be referred to as white, yellow, and blue lupines. The first step of improvement was obtained by gradual selection for larger size of the plants and size of the seeds. This also led to a considerable improvement of the quality of the seeds, the thick seed coat in large seeds being proportionately smaller in relation to the valuable interior part than in forms with small seeds. In spite of this improvement and the high protein content of the seeds these plants were almost impossible to use on account

of a high concentration of bitter and poisonous alkaloids.

As seeds free of alkaloids are known in other leguminous plants, v. Sengbusch, supported by the principle of parallel variation in different species (known already by Darwin and de Candolle and further elaborated by Vavilov), developed chemical standard methods which allowed a search on a very large scale for individuals free from alkaloids. The attempt was successful, and the second and most important step on the way from wild plant to cultivated plant was accomplished in a relatively short time by the finding of six sweet lupine individuals, representing all three original species.

The third step in improvement was taken when v. Sengbusch and Zimmermann from a total of about 10 million plants succeeded in finding a single individual in which the ripe pods remained closed instead of opening before the harvest. However, the improvement was not as useful as might have been expected because the pods, though unopened, tended to break off from the axis of inflorescence. By further search a plant was found in which the pods remained attached.

A fifth step of improvement was taken when selection led to individuals in which the seeds were ready for germination immediately after ripening instead of remaining dormant for some time. To avoid excessive moisture it was an advantage to find mutants with short hairs on the pods, or hairs which break off before maturity. Further improvements are represented (*a*) by forms in which the inflorescences are elevated above the green parts of the plants, (*b*) by forms with white seeds, which are also better adapted to regions with higher humidity and higher lime contents in the soil than the original types, (*c*) by forms with a more rapid juvenile development or increased vigor, giving rapid coverage of the soil and higher yields, (*d*) by forms with only one inflorescence which have a uniform ripening of the seed in contrast to ramified plants with several inflorescences, which ripen their seeds at different times. Thus, in a very short time about ten steps of improvement have been taken in this material, which in this way has been transformed from the wild state to a cultivated plant of great importance. The task which is now most urgent is to develop types with resistance to various diseases.

Although it does not seem quite clear that all these steps of improvement are really due to new mutations and not to segregation of rare genes already present in the population, it is obvious that this work very well illustrates the importance of spontaneous mutations in the development of cultivated plants.

D. Plant Breeding by Means of Induced Mutations

A new important method of plant breeding, which is coming more and more into general use, is the induction of new mutants in agricultural plants by treatment with x-rays or other mutagens. The literature in this field is rapidly increasing and cannot here be considered in detail. It may suffice to refer to Schwanitz's book (1957) and to some of the summarizing papers by Å. Gustafsson, the pioneer in this field, and his collaborators (Gustafsson, 1947, 1954*a*, *b*; Gustafsson and Tedin, 1954).

The present situation in this field of research may be summarized thus:

1. By various kinds of mutagens it is possible to get an unlimited number of new mutants in all cultivated plants.

2. The majority of the mutants are inferior in vigor or fertility and many of them (such as most chlorophyll mutants) die at an early stage. Among the mutants there are, however, continuous transitions between lethality and quite normal vigor.

3. Most mutagens induce "true" gene mutations and structural changes of the chromosomes simultaneously, but some new chemical mutagens have been found which seem to induce point mutations but as a rule do not break the chromosomes. Thus, different mutagens influence the genotype in different ways. Certain possibilities to direct the mutation process begin to appear.

4. The new characters induced by mutagens are of essentially the same kind as those causing the spontaneous polymorphism in our cultivated plants. Hence, the induced changes, which affect all imaginable morphological and physiological properties of the plant, open up enormous possibilities for future plant-breeding work.

5. In a few cases the induction of mutations has already led to products of economic importance, which are now on the market. There is good reason to assume that the number of such products will continuously increase.

E. The Significance of Polyploidy in the Evolution and Breeding of Cultivated Plants

a. Advantages of Polyploidy:

Darwin did not know anything of chromosomes and, consequently, the wide field of polyploidy in higher plants was also a shut book to him. As is well known, multiple chromosome numbers often occur in wild species of angiosperms and are still more frequent among cultivated plants. The reason for this is undoubtedly that many polyploids, which have arisen spontaneously, have been selected by man on account of their useful properties. This raises the question as to why the polyploid cultivated plants are more valuable than related types with lower chromosome numbers. This is a comparatively complicated problem. An increase in chromosome number leads to an increase in cell size and not infrequently also to an increase in organ size. Changes in cell volume have far-reaching consequences with regard to the physiology, metabolism, and fertility of the plants. As demonstrated by Schwanitz (1953) these changes are predominantly deleterious especially in pure autoploids. At least in part the harmful effects may be removed by recombination, and in this way a cell-size increase beyond the optimum may be reduced to more proper dimensions.

Another essential factor is that polyploids frequently have increased powers of adaptation, and an increased ability to develop extreme gene combinations. This is especially true of alloploids, which tend to combine the ecological abilities characteristic of the separate genomes of which they are composed.

A third cause of superiority of polyploids has been stated by Melchers (1946). He pointed out that autopolyploids with more than two chromosomes of each kind may carry a larger number of genes of selective value than diploids. This will lead to a wider range of gradations in the polyploids, not only of genes with morphological effects but also of genes with physiological effects of adaptive importance.

The literature on polyploidy in relation to the origin of cultivated plant species is comprehensive and cannot be discussed in detail. Reference may be made to the summarizing works by Schwanitz (1954, 1955, 1957) and Müntzing (1956, 1957). The following points, however, should be briefly discussed:

b. Cases of Resynthesis of Already Existing Polyploid Cultivated Plants:

The very best way to elucidate the genomatic constitution of a polyploid species is to resynthesize the species. This has, indeed, been tried with more or less success in several species of polyploid cultivated plants. Müntzing (1956, 1957) reviews such cases in *Nicotiana, Gossypium, Triticum, Brassica, Phleum,* and *Dactylis.* Let us now confine ourselves to a few of these cases. As is well known, and as was first detected by Sakamura (1918), the wheat genus *Triticum* comprises species with the somatic chromosome numbers 14, 28, and 42. Thanks to McFadden and Sears (1946) and to Kihara and his collaborators (Kihara, 1949; Kihara and Lilienfeld, 1948; 1949; Kihara, Okamoto Ikegami, Tabushi, Suemoto, and Yamane, 1950), it is now clear that the hexaploid wheat species represent a combination of tetraploid wheat with the genome present in *Aegilops squarrosa.* Although quite typical bread wheats have not yet been synthesized in this way, the origin of the hexaploid wheat species has in the main been solved.

In the genus *Brassica* the resynthesized polyploids can scarcely be distinguished from the spontaneous ones. The rape, *Brassica napus,* has 38 chromosomes and has been synthesized by U (1935), Rudorf (1950), Frandsen (1947), Olsson (1953), and by Olsson, Josefsson, Hagberg, and Ellerström (1955) from crosses between *B. campestris* with 20 chromosomes and *B. oleracea,* having 18 chromosomes.

The great similarity between the synthetic and spontaneous strains of rape may imply that rape is a cultivated plant of recent origin. In their chromosome atlas of cultivated plants (1945), Darlington and Janaki-Ammal state that *B. napus* arose about 1680. Rudorf (1950), however, points out that *Brassica rapa* has probably arisen repeatedly in various areas and involved various parent strains. This is indicated by the large differences between German and Polish varieties. Moreover, the varieties from eastern Asia probably originated independently of the European varieties.

Fertility in the synthetic strains of rape may be perfect from the beginning or may be rapidly improved by selection; and fertile hybrids between the spontaneous and synthetic strains can be produced without difficulty. In the offspring of such hybrids there is only a moderate degree of segregation.

Just as autopolyploidy is of importance among wild plant species it is also met with in some cultivated plant species such as timothy, *Phleum pratense*, and cocksfoot, *Dactylis glomerata*.

The constitution of *Phleum pratense* has been studied especially by Nordenskiöld (1945). The species is hexaploid and genome-analytical studies have revealed that all three genomes can pair with each other without difficulty. They are also homologous to the single genome present in the related diploid species, *Phleum nodosum*. Nordenskiöld consequently concludes that *P. pratense* is strongly autopolyploid.

The question about the constitution of timothy may now be considered to be solved by a second paper Nordenskiöld (1949), in which she describes the synthesis of autohexaploid derivatives of the diploid *P. nodosum*. These new hexaploids were morphologically similar to *pratense*, had good fertility and could be crossed with *pratense* without difficulty.

The resynthesis of different polyploid cultivated plants is, of course, primarily of theoretical interest but in some cases successful attempts have already been made to utilize the new products in practical plant breeding. This is fairly easy in a material such as rape, in which spontaneous and synthetic strains intercross without disturbances of any kind. Consequently, new and valuable genes for frost resistance or disease resistance may be introduced and lead to valuable new strains. Definite results of this kind have already been obtained in cotton.

c. Experimental Production and Spontaneous Origin of new Polyploids Previously Unknown:

Especially during the last twenty years (after the discovery of the chromosome doubling effect of colchicine by Blakeslee and Avery, 1937 and by Nebel, 1937) a large amount of work has been carried out in order to produce new kinds of polyploids of economic importance. During this work a varied general experience has been gained, the most important details of which may be briefly formulated thus:

1. The new products of induced polyploidy are generally bad, and only in rare cases do they represent an immediate advance.

2. The starting material must be large and comprise a series of different biotypes.

3. The immediate products of chromosome doubling must be improved by recombination and selection.

4. Allogamous strains are in this respect more favorable than autogamous material. The automatic recombination always going on in cross-fertilizing species considerably facilitates the attainment of products with valuable properties.

5. There is a comparatively narrow range within which a change in chromosome number is favorable or at least tolerable, and the optimal chromosome number is situated at different levels in different species. The degree of polyploidy may be increased to a higher degree in alloploids than in autoploids.

6. Polyploid breeding is more likely to be successful in material in which some vegetative part of the plant represents the useful product. The reason for this is that most induced polyploids and especially the autoploids tend to have a reduced fertility.

7. All induced polyploids have other norms of reaction than the corresponding diploids.

d. Some Economically Important Products:

Good examples of valuable spontaneous polyploids are to be found among *ornamental plants*, especially when they are capable of vegetative propagation.

Until 1885 the *Narcissus* varieties in the Netherlands were mainly small-flowered diploid forms with $2n = 24$. From this time onwards the diploids were gradually replaced by the newly arisen and more magnificent triploid forms, and around the beginning of this century big-flowered tetraploids began to appear, which in their turn replaced the triploids.

Also in the development of garden varieties in the genus *Iris* polyploidy has been of great importance. During the interval 1840–1910 almost all varieties were diploids with 24 chromosomes, but after 1895 some triploid varieties also began to appear. After 1910 the leading varieties were predominantly tetraploid, and among 109 varieties, which in 1943 were considered to be the best ones, 108 were tetraploid and only 1 triploid. Diploid varieties were completely lacking. There are also now some pentaploid and aneuploid (supertetraploid) varieties, which are economically important. All these polyploids, representing a mixture of auto- and alloploids, are derived from several different species of *Iris* but in the first place from the diploid *Iris variegata* and *Iris pallida*. Detailed information concerning origin and cytology of the different *Iris* varieties is given by Stern (1946).

Similar stories might be reported for other genera of ornamental plants such as *Chrysanthemum, Gladiolus, Dahlia,* and *Cyclamen.* In all these cases polyploids have arisen spontaneously. However, a few cases are also known in which polyploids have been experimentally induced. One such case has been reported by Emsweller (1947) with regard to the American easter lily, *Lilium longiflorum.*

A very good case of breeding by means of induced polyploidy in a fruit plant is represented by Kihara's work on triploid water melons (Kihara, 1951). In *Citrullus vulgaris* ($2n = 22$) colchicine-induced tetraploids were obtained and intercrossed with diploids. Only in the direction tetraploid × diploid were seeds obtained capable of germination. On account of poor quality these seeds give the seedlings a poor start, but after a month the triploid plants surpass the diploids as well as tetraploid parents and give a rich yield. In different combinations the yield of the triploids was found to be from 30 to 97 per cent higher than that of the diploids, and sugar content as well as texture was found to be satisfactory.

Beets and turnips. Good results with induced polyploidy have been obtained in beets as well as turnips. With regard to triploid and tetraploid sugar beets and mangels there is already a fairly comprehensive special literature starting from about 1938. It was soon generally agreed that the tetraploid beets with 36 instead of 18 chromosomes are somewhat inferior to the diploids, this inferiority being especially correlated with a too slow rate of development in the tetraploids. Quite recently, however, Rasmusson (1953 and unpublished) has obtained some highly interesting results which demonstrate that after a long period of selection useful tetraploid strains may be obtained. These strains have not only reached the level of the diploids but also slightly but significantly surpassed it. So far, however, the tetraploid beets are not used in practice.

On the other hand it was realized about twenty years ago that triploid beets are quite good and give a higher yield than the corresponding diploids. Fortunately triploids can be produced on a large scale by bulk crosses between selected diploid and tetraploid strains, and when such a material is used by the farmers, a significant increase in sugar yield per area is obtained. Therefore, such "poly-Betas" are now cultivated in the sugar-beet fields in several countries in Europe, and work with such material is also carried out in Japan.

In another root crop, turnips, *Brassica campestris rapifera,* autotetraploid strains with 40 instead of 20 chromosomes have been produced and studied by Levan and Josefsson (*cf.* Josefsson, 1955). The main result of this breeding work is the Svalöf "Sirius" turnip, which came on the market in 1953. It is the result of intercrossing of three different tetraploid strains, followed by a strong selection, and is almost surprisingly superior to the diploid related varieties in both root weight and dry matter weight.

The examples given may be sufficient, and it should only be added that favorable results with induced polyploids have also been obtained in certain clover species and in rye (*cf.* Müntzing, 1956; 1957).

e. Conclusion:

Thanks to comprehensive cytogenetic research in a series of different polyploid cultivated plant species, it has been demonstrated that these species are derived from related species with lower chromosome numbers. In some cases it has even been possible to find the original parents and to resynthesize the polypoid species approximately or accurately. In such cases we have to deal with allo- as well as autoploidy.

In many cases the polyploid cultivated plants are evidently quite old, and we do not know with any certainty when they arose. However, especially in ornamental plants the evolution of polyploidy is quite recent, and it is now possible to analyze how and when this process really occurred. However, all these forms arose spontaneously and were only selected on account of their valuable properties. Not until later was it realized that they were polyploid and that in several cases they had entirely replaced their diploid progenitors.

From such a situation it is not far to a conscious breeding of polyploids. This direct way, however, could not be used until the phenomenon of polyploidy had been carefully studied and good methods had been evolved for the production of allo- as well as autoploids. This has now occurred and today we can survey what polyploid breeding in the strict sense has so far been able to accomplish. Indeed, if we consider that this line of work is not more than about twenty years old the total results are not discouraging. Evidently

this work has progressed far enough to allow the conclusion that breeding involving induced polyploidy, parallel to other breeding methods, will have an important role to play in the future. It should be stressed once more, however, that this method is not of general application. Only under certain circumstances and in some species are there chances for the production of something new and valuable. But in such cases the success may sometimes be considerable.

F. Utilization of Hybrid Vigor

Already in his great book of 1886 Darwin repeatedly discusses the evil effects of inbreeding and the beneficial effects of crosses between unrelated individuals or different races. As animals and plants behaved essentially alike in this respect, Darwin was convinced that it is a great law of nature that long-continued close inbreeding is injurious, whereas crossing is beneficial. This conclusion was further supported by the results of his comprehensive experiments on the effects of cross- and self-fertilization in the vegetable kingdom (1876). As we have seen (*cf.* p. 198), Darwin believed that the fundamental cause of these phenomena was the variation in the conditions of life to which all individuals are exposed, and that these exterior influences by means of modified gemmules caused a differentiation of the sexual elements. "Whatever affects an organism in any way, likewise tends to act on its sexual elements," says Darwin.

Though we no longer accept this conclusion, and the effects of inbreeding and outcrossing are now explained in a different way, we still agree that hybrid vigor and degeneration resulting from inbreeding are of paramount importance not only for the life of the wild organisms but also for the production of good domestic animals and high-yielding cultivated plants.

Already at Darwin's time hybrid vigor was utilized in animal breeding, and this is still the case today, though probably the great economic possibilities of this type of work have not yet been fully exploited. In plant-breeding work, on the contrary, hybrid vigor is very much utilized, especially in cross-fertilizing plants, but in recent years higher yields by outcrossing are obtained also in some spontaneously self-fertilizing species.

The best example of a successful utilization of hybrid vigor in a cultivated plant is that afforded by the breeding of maize in the United States. The basic research was carried out by Shull, East, and Jones in the beginning of this century, and by a brilliant cooperation between a large number of workers it has been possible to get a large and valuable collection of inbred lines, which is being continually improved (*cf.* Mangelsdorf, 1951). By different types of intercrossing of these lines and their hybrids high-yielding products are obtained, which have enormously increased the yield of maize. Of the maize material cultivated in 1944 in the corn belt of United States 83 per cent was hybrid corn, and cultivation of this hybrid material led to an increase in yield of about 600 million bushels.

This enormous development has taken place during the last twenty-five years. In 1933 very little hybrid corn was cultivated, but in the following years the percentage of the maize area in which such material was used rapidly increased, and in 1951 it had almost reached 80 per cent.

Similar methods are now, of course, used in most other countries in which maize is grown, and the utilization of hybrid vigor is also practiced in many other cultivated plants. The importance of this for the supply of food to the world's increasing population is obvious.

4. DOMESTICATION CHARACTERS IN PLANTS

We have seen above (pp. 207–208) that the difference between domestic animals and their wild progenitors and relatives are in part caused by purely environmental modifications, but to a large and more important extent they are genotypic. Owing to strong and prolonged selection, some domestic animals have been transformed to such an extent that they are now dependent on man and would not survive under natural conditions. In some cases the products of human selection are abnormal and clearly pathologic.

In cultivated plants we meet entirely similar conditions. Giant properties are frequent and are often caused by polyploidy, especially with regard to the size of flowers and seeds. However, in some cases similar effects are obtained by gene mutations or possibly by internal changes in the chromosomes of an endopolyploid nature, as assumed by Schwanitz (1957: 15–16). The giant characteristics, ultimately caused by an increased size of the cells, involve as a rule not only a considerable increase in yield but also a great improvement in quality. The increase in yield is also made possible by a larger total leaf surface and hence a more intensive metabolism.

Specific domestication characters, which are frequent in plants, are, for instance, (*a*) loss of the natural modes of seed (and tuber) dispersal, (*b*) loss of bitter poisonous substances, (*c*) loss of mechanical means of protection, (*d*) loss of the period of dormancy in newly formed seeds. All these changes (the details of which I may refer to Schwanitz, 1957) obviously reduce the ability of the species to exist under natural conditions, and the same is true of specific changes in the shape of the roots, stems or leaves, which are now useful for human consumption.

Changes in the floral region, for instance double flowers, often lead to sterility, and this may also ensue from other causes such as triploidy, aneuploidy, or the action of specific genes. Products of this kind can only survive by vegetative propagation and, thus, a very large part of our ornamental flowers and fruit-producing plants, which are of essential value to our culture, are obvious abnormalities which would immediately disappear if they were left to the purifying action of natural selection. Thus there is a very good parallel between plants and animals with regard to the nature of the useful characters which man has been able to induce. However, the mechanisms of induction and preservation of such changes are partly different, polyploidy and vegetative propagation being important in cultivated plants but not in domestic animals.

IX. SUMMARY

1. With regard to the effects of environment on animals and plants present-day views differ fundamentally from those of Darwin. He was unable to distinguish between phenotype and genotype, nor did he know the difference between environmental modifications and variations conditioned by a change in the hereditary constitution. Another important difference between our views and those of Darwin is that the latter did not know the mechanisms of recombination and that hereditary changes are of two kinds, those depending on recombination of already existing genes and those caused by mutation.

2. Darwin's thesis that species when domesticated start to vary on account of the variable conditions of life and excess of food is essentially or entirely wrong. Variation is not increased, but the changed environment allows the survival of many types which are of interest to man, but which in the wild state are removed by natural selection.

3. Though Darwin wrongly believed that variability is predominantly caused by environmental influences, it should be emphasized that he stressed the point that the constitution of the organisms will largely decide what kind of change will be induced. Thus, the organisms were supposed to have special constitutions which, though easily affected and changed by environmental influences, have a certain limited degree of independence.

4. Darwin's conclusion that acclimatization is accomplished by spontaneous variation, aided by habit and regulated by natural selection, is for the most part correct. The incorrect part is "aided by habit," as this statement implies not only individual noninherited modifications, which certainly also play a role in acclimatization, but also the gradual fixation and inheritance of such changes. If Darwin had known better the different mechanisms involved in spontaneous variation, his views on acclimatization would have been still more adequate.

On the foundations laid by Darwin other workers have later succeeded in elucidating still further the problem of acclimatization and adaptation. It is now clear that these processes are correlated with a far-reaching differentiation within the species, which represents genotypic adaptations to different kinds of environment. In some species this differentiation is purely genetic and based on recombination of multiple genes. In other groups differences in the number or structure of the chromosomes may be involved.

5. To a surprising degree Darwin and his contemporary animal breeders were familiar with the favorable effects of crossing; and the increased vigor of F_1 hybrids was even utilized commercially, such animals being produced for immediate consumption. Darwin states that a good result of such intercrossing is obtained, if the individuals combined are either innately of different constitution or have been differentiated by exposure to dissimilar conditions. The latter part of the statement is incorrect, as Darwin, following Lamarck, believes that an immediate action of the environment will influence the constitution.

6. To Darwin reversion, the reappearance of characters from earlier generations, was a concept almost as important as inheritance itself. He found that crossing is a potent means of inducing reversion and believed that the act of crossing in itself tends to bring back long-lost characters. Thus, crossing was regarded as a disturbance in

the organization, which upsets the constitutional equilibrium in such a way that latent characters may reappear. Darwin's views in this respect, and his failure to grasp the mechanism behind a monohybrid segregation observed by himself, makes it easier for us fully to realize the greatness of Mendel's results. Thanks to him we know that variability after crossing is not due to a disturbance of the sexual functions but to recombination of stable units of heredity. This mechanism also easily explains the reversions, whether occurring in F_1 or later generations.

7. In other respects we can largely agree with Darwin concerning the effects of crossing, e.g., with his statements that crossing between two breeds sooner or later gives an intimate blending, and that uniformity within a domestic race is obtained when there is opportunity of free intercrossing. These empirical facts are now interpreted on the basis of recombination of multiple genes, which Darwin did not know.

8. Though Darwin had a thorough knowledge of the empirical results gathered in inbreeding work, he was not able to give any plausible interpretation of these phenomena. Present-day genetics not only explains why vigor and fertility are correlated with heterozygosity and homozygosity for numerous recessive factors but also why inbreeding leads to a morphological differentiation of the material.

9. From his descriptions it is clear that Darwin had repeatedly seen or heard of effects caused by single mutant genes. Such cases could not be convincingly accounted for by the gemmule hypothesis, and Darwin was forced to admit that the organisms have an important interior constitution, which is not only an image of the exterior properties but which obeys mysterious and unknown laws, which he did not succed in solving.

10. Darwin's views on the importance of different kinds of selection for the origin of improved types of domestic animals and cultivated plants are still quite correct. Modern genetics has amply confirmed that as long as biological material is genetically heterogeneous, selection may lead to surprisingly great changes. In two respects our views on selection today differ from those of Darwin. We know that environmental variations are not inherited and that genetic polymorphism is not always or entirely the result of selection. In small populations random distribution of genes, genetic drift, may also occur.

11. The only criticism which can be directed against Darwin's views on the origin and development of domestic species concerns his conviction that variability, on which the possibility of selection rests, mainly depends on changed conditions of life, though governed by complex and unknown laws. Otherwise his argumentation is essentially correct, and his observations and conclusions are, indeed, of fundamental importance for all later investigations in this field of research.

12. Though many new data have accumulated since Darwin's time nothing essentially new, regarding the origin of domestic animals from wild species and their improvement by selection, has really developed. The most interesting data have been obtained from the breeding of some young domestic animals, in which it has been possible to follow their behavior under domestication step by step from the beginning. Good cases of this kind are represented by the domestic rabbit and newly domesticated fur animals, such as fox and mink. In these animals we can follow how a gradually increasing polymorphism is obtained by mutation, recombination, selection and inbreeding.

13. The higher productivity as well as all other domestication characters are in part environmental modifications, resulting, for instance, from the increased amount of food given to the animals. To a still higher degree they are the result of a changed genotypical constitution. Often the characters induced are not only one-sided and driven to extremes but are also correlated with obvious disharmonies or pathologic alterations.

14. The oldest domestic animals are supposed to have had a polyphyletic origin, whereas with regard to all younger ones there is more or less conclusive evidence that they are monophyletic. In cases where it still seems justifiable to speak of a polyphyletic origin the ab-original species are closely related and sometimes quite interfertile. In such cases it is a matter of taste whether a domestic species should be considered mono- or polyphyletic.

15. As already realized by Darwin, the cultivated plant species have gradually evolved from wild relatives, and for the majority of them their wild relatives can be indicated with certainty. Distinction may be made between primary and secondary cultivated plants. An especially interesting group of secondary cultivated plants are those which, before being brought into culture, occur as weeds in the fields of primary cultivated plants. The occurrence of centers of polymorph-

ism, regarded by Vavilov to be centers of origin, is discussed.

16. A review is given of different mechanisms of development of our cultivated plants and of some important plant-breeding methods. The oldest method, selection in genotypically variable, cross-fertilizing plants was well known to Darwin and excellently illustrated by the production and successive improvement of the sugar beet in the nineteenth century. Other methods, unknown to Darwin but now of great importance, are breeding by crossing and recombination, utilization of spontaneous and induced mutations and of spontaneous and induced polyploidy. Hybrid vigor is now widely utilized in the breeding of cultivated plants.

Thus, Darwin was only familiar with a minor part of the mechanisms involved in the origin of our cultivated plants and, for instance, did not know anything about the high frequency of polyploids among such plants. The difference between our knowledge and views on variation under domestication and those of Darwin are therefore more pronounced with regard to cultivated plants than with regard to domestic animals.

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ISOLATION AS AN EVOLUTIONARY FACTOR

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INTRODUCTION

THE fact that isolation plays a role in evolution was recognized long before Darwin (Buch, 1825). What this role is, however, was frequently misunderstood. Even today there is so much difference of opinion on this point that it would be hasty to assert that a complete solution is within our grasp.

One might treat this important subject by giving a straightforward analysis of the various problems associated with isolation and the current attempts at solution. I prefer a different treatment. Most of the great pioneers of modern evolutionary thinking, Darwin, Wallace, Huxley, Weismann, Wagner, de Vries, and others, grappled with this difficult theme, and it would seem a fascinating task to trace their steps and to determine where they advanced our understanding and where they "missed the boat" and why. There are few other subjects in biology which lend themselves as well to historical treatment as the subject of isolation. An analysis of the questions asked by each generation of investigators and of the reasons for some of the wrong answers they gave, time after time, will lead to a much fuller understanding of the problems than would a systematic treatment of isolation.

Darwin's[1] voyage on the *Beagle* gave him abundant opportunity to observe isolation at work:

> . . . barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the production of various regions . . . on the opposite sides of lofty and continuous mountain-ranges, of great deserts and even of large rivers, we find different productions (Darwin, 1872: 414).

When chided by M. Wagner for underestimating the role of isolation in speciation, Darwin defended himself with the words: "It would have been a strange fact if I had overlooked the importance of isolation, seeing that it was such cases as that of the Galapagos Archipelago, which chiefly led me to study the origin of species" (*Life and Letters of Darwin* **3**: 159, letter of October 13, 1876). Yet, there is no doubt that Wagner's criticism was justified. Darwin admitted the occurrence of speciation on islands, but he emphasized again and again that incipient species could evolve into full species also without any spatial isolation:

> I can by no means agree [with Wagner] that migration and isolation are necessary elements for the formation of new species (1872: 106). . . . I believe that many perfectly defined species have been formed on strictly continuous areas (1872: 175).

All the evidence that has accumulated since Darwin indicates that this assumption is unwarranted as far as higher animals are concerned. It is of more than historical interest to determine how Darwin arrived at his erroneous conclusion. An analysis of his publications and letters indicates that responsible for it was his failure to understand clearly four evolutionary phenomena or concepts.

(*a*) *The Meaning of the Term "Variety."* Since species to Darwin were the result of gradual evolution they had to pass through an intermediate stage, such as the "incipient species" and the

[1] Darwin's contribution to the subject is particularly difficult to evaluate since he was more plagued with doubts on this than on almost any other evolutionary question. As Barzun (1948) has remarked, not without justification, Darwin was often loath to commit himself too definitely, and if he made an emphatic statement in one sentence, he tended to take part or most of it back in the next. This is surely true for his stand on isolation and makes a balanced account quite difficult. I believe, however, that the quoted sentences represent Darwin's basic views.

"variety." "A well-marked variety may be called an incipient species" (Darwin, 1872: 54). With the variety occupying such a key position in the problem of the origin of species, one might expect that Darwin would have devoted a great deal of effort to a definition of the concept and to an investigation of the circumstances under which varieties are being formed, but this is not the case. Darwin simply took over term and concept as it was current among the naturalists and systematists of his period. He never seems to have realized that since Linnaeus (and even before) the term had been applied indiscriminately to two very different kinds of phenomena, deviating individuals and deviating populations. Weismann, as we shall presently see, fell into the same error. For a typologist any deviation from the type is a "variety." For a biologist, on the other hand, it is of vital importance to know whether such a deviant is merely an intrapopulation variant or a different population. If Darwin had made a clear distinction, he would not have said: "If a variety were to flourish so as to exceed in numbers the parent species, it would then rank as the species, and the species as the variety; or it might come to supplant and exterminate the parent species; or both might coexist, and both rank as independent species" (1872: 54).

(*b*) *A Morphological Species Concept.* In view of Darwin's great insight into biological processes and evolutionary phenomena, one is somewhat shocked to realize how completely his species definition is based on degree of difference:

> . . . I look at the term species as one arbitrarily given, for the sake of convenience, to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms (1872: 54) . . . the amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties (1872: 58).

Weismann (1872: 19), who argued along exactly the same lines as Darwin expressed the matter as follows: "The species is nothing absolute, and the differences among various species are of exactly the same nature as the differences between the sexes of one and the same species." It is on the basis of views like this that de Vries eventually developed his theory of speciation by mutation. I have looked in vain in Darwin's writings for an indication that he ever considered the species as anything but a "more distinct variety." Not realizing that the species is a "reproductively isolated population," a concept which was definitely familiar to many of his contemporaries (Mayr, 1957*a*), Darwin was quite unable to focus on the essential aspects of speciation and on the role of isolation. And yet, the same Darwin had extremely sound ideas on the development of sterility in incipient species (see below).

(*c*) *Failure to Distinguish Between Phyletic Evolution and Multiplication of Species.* Evolutionary change within a lineage will, given enough time, produce sufficient change to justify ranking the descended population as a species different from the ancestral one. This is the "formation of a new species" of which Darwin spoke most frequently in his work. But this process of evolutionary change fails to account for the steady increase in the number of species which seems to have occurred in geological history. The splitting off of one lineage from another, the "multiplication of species," includes an evolutionary factor (the acquisition of reproductive isolation) which is not implicit in mere evolutionary change. Owing to his essentially morphological species definition, Darwin failed to give sufficient emphasis to the problem of the origin of reproductive isolation. Where he was concerned with the origin of sterility among species, it was in connection with "natural selection" rather than with speciation.

The failure of Darwin, and later of Weismann, to understand the real scientific problems of the origin of species, because of their failure to understand the biological nature of species, should be an object lesson to those who attempt to minimize the species problem. Even though we have made great progress in this field during the past thirty to fifty years, it would be premature to believe and to assert that we understand the nature of species of all kinds of organisms, or on the other hand, to claim that it is useless to seek an understanding.

(*d*) *A Desire for a Single Factor Explanation.* Evolutionists prior to about 1930 were singularly reluctant to consider the interaction of various factors in the causation of evolutionary phenomena. Weismann (1872) bases his entire discussion on the alternative "natural selection *or* geographical isolation" as the factor responsible for the origin of new species. Darwin states, "Although isolation is of great importance in the production of new species, on the whole I am inclined to believe that largeness of area is still more

important" (1872: 107). He supports this claim by arguing that in large areas there are more individuals and, thus, "there will be a better chance of favorable variations" and also, "the conditions of life are much more complex from the large number of already existing species" (1872: 107), and that this also will favor the origin and spread of new "varieties." Admittedly all this would favor phyletic evolution, but it does not shed light on the origin of reproductive isolation. In acknowledging Wagner's volume on geographic isolation (*Life and Letters of Darwin* **3**: 157), Darwin admits the importance of this factor but then continues,

> I must still believe that in many large areas all the individuals of the same species have been slowly modified, in the same manner, for instance, as the English race horse has been improved, that is by the continued selection of the fleetest individuals, without any separation.

Did Darwin not see that there is no stricter isolation of gene pools than exercised by the animal and plant breeders? What would have happened to the selection of race horses, if they had been permitted to interbreed freely with ponies, jumping horses, draft horses, and all sorts of utility horses? This very example should have convinced Darwin completely of the indispensibility of isolation, yet he used it to argue against the importance of isolation because he felt he had to make a choice between either isolation or selection. And this is the same Darwin who said elsewhere (1868: 185):

> On the principle which makes it necessary for man, whilst he is selecting and improving his domestic varieties, to keep them separate, it would clearly be advantageous to varieties in a state of nature, that is to incipient species, if they could be kept from blending. . . .

One would expect Darwin to continue "by spatial segregation." Instead he concludes, "either through sexual aversion, or by becoming mutually sterile." The mechanism by which coexisting varieties might acquire sexual aversion or mutual sterility is not indicated. Darwin concludes his rejection of Wagner's thesis with the emphatic statement: "My strongest objection to your theory [of geographic speciation] is that it does not explain the manifold adaptations in structure in every organic being" (*Life and Letters* **3**: 158), as if speciation and adaptation were exclusive phenomena.

WAGNER, HIS FOLLOWERS AND OPPONENTS

The most ardent champion of isolation in the evolutionary literature is the great naturalist Moritz Wagner (1813–1887). During his travels in Asia, Africa, and the Americas, he had observed that, almost invariably, closely related forms or species occupy adjacent ranges, separated from each other by rivers, mountain ranges, valleys (in the case of mountain species) or, indeed, by any barrier to dispersal. He first published this observation in 1841, elaborated it in a major essay in 1868 and added to it in a number of later essays, republished posthumously in 1889. While Darwin had readily agreed that geographic isolation favors speciation, Wagner insisted that it was a *conditio sine qua non*:

> The formation of a genuine variety which Mr. Darwin considers an "incipient species," will succeed in nature only when a few individuals can spatially segregate themselves for a long time from the other members of the species by transgressing the confining barriers of their range (1889: 64).

It is crucial for an understanding of the controversy between Wagner and Weismann to realize that Wagner, when speaking of a variety as an incipient species, referred without exception to geographic races while Darwin and Weismann in similar arguments more often than not referred to intrapopulation variants. In view of Wagner's incessant repetition of the two terms migration and colonization as the principal factors responsible for the origin of new species, it may be pertinent to quote a modern author, who has probably never read Wagner: "Thus, migration and colonization favour the origin of discontinuity" (Darlington, 1956: 362).

Wagner's original observation (the geographic relation of incipient species) and the empirical conclusion he drew from this observation (the importance of geographic isolation for speciation) are as true today as they were when first published. Wagner, however, was not quite so successful when he tried to find reasons for the need of geographic isolation. He advances two reasons. The first is, to prevent the new population from being swamped by the parental one:

> The origin and continued evolution of a race will always be endangered where numerous reinvading individuals of the same species disturb this process by general mixing and, thus, usually suppress it altogether. . . . Without a long continued separation of the colonists from the other members of their

species the formation of a new race cannot succeed in my opinion (1889: 65).

This first conclusion is not only substantiated by observation but has been confirmed by much recent work in population genetics which has established the overriding importance of integrating factors in an isolated gene pool.

Wagner was less successful in the second half of his explanation. He firmly believed that a change of environment was necessary for natural selection to become active. "Organisms which never leave their ancient area of distribution will never change" (1889: 82). Even though it is, of course, true that there is less probability of evolutionary change in a stable environment, natural selection (even if only normalizing selection) will always be active and phyletic evolution will frequently take place. These marginal and ill-conceived comments on the relation between isolation and natural selection served Weismann (1872) as the basis for a severe criticism of Wagner's theory of geographic speciation. The original question, "Can species multiply without geographic isolation?" was changed into the questions, "Is isolation itself the factor which is responsible for the changes in isolated populations?" and, "Is isolation necessary for varieties to become constant?" Weismann's refutation of Wagner, like Darwin's, is based on a morphological species definition and on the assumption that a morphologically different variety is an incipient species. He states that, on the basis of Wagner's theory, on one hand all isolated populations of species should be different varieties and, on the other hand, different varieties should not be able to originate in the same area as the normal type of species. Both of these postulates can, of course, be easily disproved. Failure of geographic speciation, he says, is indicated by the many cosmopolitan species, particularly among the tardigrades and the fresh-water crustaceans, but also among higher organisms (for instance, the butterfly *Vanessa cardui*). On the other hand, Weismann continues, there are numerous cases of polymorphism, particularly among the butterflies, which prove that varieties can originate without isolation. How much in his argument he equates morphological change with origin of new species may be documented by some quotations. He asks, is it possible "that newly arising characters can become constant only through isolation and subsequent colony formations and thus give cause to the origin of a new species?" (1872: 6) and asserts in a statement of *non sequiturs*: ". . . it would be a fatal mistake if one were to assume . . . that isolation were an indispensable prerequisite to the modification of species, that not selection, but isolation alone would make possible the change of a species, that is its splitting into several forms" (1902: 319). One final quotation may demonstrate how completely Weismann missed the essential point in the problem of the multiplication of species:

> In this it is quite unimportant how they [endemic species that originated in isolated areas] originated, whether by Amixia in a period of variation or by natural selection, which tried to adjust the immigrants to the new environmental conditions of the isolated area. The change can even have been caused by influences which had nothing to do with the isolation, as for example the direct influence of the physical environment or the process of sexual selection (1872: 107).

The main reason for Weismann's inability to evaluate properly the role of isolation was his failure to determine what an incipient species is. This was seen much more clearly by his successors and explicitly or implicitly it forms the basis of most discussions of isolation during the 1880's and 1890's. From the very beginning to the present day there has been a clear separation of two schools of thought. On one side there are those who, with Wagner, insist that geographic isolation is an indispensable prerequisite for the multiplication of species in sexually reproducing organisms (excluding the special situation of polyploidy); on the other side are those who insist with equal determination that in addition to geographic speciation there exist various modes of sympatric speciation. The sympatrists claim that varieties with all the properties of incipient species often coexist. Their argument was, for the first time, clearly stated by Darwin himself:

> I can bring forward a considerable body of facts showing that within the same area, two varieties of the same animal may long remain distinct, from haunting different stations, from breeding at slightly different seasons, or from the individuals of each variety preferring to pair together (1872: 105).

Wallace (1889: 150) enthusiastically supports this contention and concludes

> that geographical or local isolation is by no means essential to the differentiation of species, because the same result is brought about by the incipient species acquiring different habits or frequenting a different station;

and also by the fact that different varieties of the same species are known to prefer to pair with their like, and thus to bring about a physiological isolation of the most effective kind.

Catchpool, Dahl, Romanes, Kellogg, and Petersen were other early authors endorsing the theory of sympatric speciation, as I have pointed out in a partial historical review of the field (Mayr, 1955). The first author who can be credited with full understanding of the difference between phyletic evolution and the multiplication of species, and who has stated the case in a thoroughly modern manner seems to have been the ornithologist Seebohm. He points out with great logical acuity that natural selection and variation alone cannot account for the multiplication of species (1888: Chap. 3):

> There is no reason why evolution should not go on indefinitely modifying a species from generation to generation until a pre-glacial monkey becomes a man, and yet no second contemporary species be originated. The origin of a second species is prevented by interbreeding. So long as the area of distribution of the species is continuous and not too large, the constant intermarriage which takes place between the males of one family and the females of another distributes the inherited and transmittable modifications throughout the race or species; which may advance or retrograde according to circumstances, but is prevented by interbreeding from originating a second species. . . . In order to originate a second species, it is necessary to counteract the leveling effect of interbreeding by isolating some of the individuals comprising the species, so that there may be two colonies, which are unable to communicate with each other, and consequently unable to interbreed. . . . In every species there is a tendency to vary in definite directions: the variations are hereditary and cumulative, so that evolution goes on steadily, though slowly, from generation to generation. If a part of the species be isolated from the rest, the evolution of the two colonies does not proceed in exactly the same direction, and the rapidity with which differentiation takes place is exactly in proportion to the difference in the circumstances in which the two colonies are placed.

How highly Seebohm rated isolation is evident from his amusing criticism of Romanes:

> It is a remarkable circumstance that only once in the seventy-five pages of Mr. Romanes's paper does the word isolation occur, and then in a footnote. In a paper relating to the origin of species it is like the play of Hamlet with the part of Hamlet omitted.

It was around this time that the concept of the species as an interbreeding community became general among naturalists and systematists. It is this concept which is taken for granted by K. Jordan in 1896 and 1905 (Mayr, 1955) and of which Poulton (1903, 1908: 68) says: "The idea of a species as an interbreeding community is, I believe, the more or less acknowledged foundation of the importance given to transition" (when in doubt whether or not two isolated populations are conspecific). This permitted a reasonable explanation of the origin of reproductive isolation during geographic isolation:

> The individuals of an interbreeding community form a biological whole, in which selection inevitably keeps up a high standard of mutual compatibility between the sexual nuclei. As soon, however, as a group of individuals ceases, for any reason, to breed with the rest of the species, there is no reason why the compatibility of the sexual nuclei of the two sets should be retained. Within each set, selection would work as before and keep up a high standard of compatibility; between the sets compatibility would only persist as a heritage of past selection, gradually diminishing as life changes of structure in either or both of the sets rendered them less and less fitted to produce fertile combinations (Poulton, 1903, 1908: 81).

Similar views were expressed by K. Jordan, D. S. Jordan, and by far the majority of systematists publishing about speciation during the first half of this century.

THE IMPACT OF MUTATIONISM

The theory of geographic speciation seemed to receive a fatal setback from the newborn science of genetics. Bateson, de Vries, and other early Mendelians believed that "species arise by mutation, by a sudden step in which either a single character or a whole set of characters together becomes changed" (Lock, 1906: 144). De Vries said at the same time, "The theory of mutation assumes that new species and varieties are produced from existing forms by certain leaps. The parent type itself remains unchanged throughout this process and may repeatedly give birth to new forms" (1906: vii). These saltationist views swayed the thinking of contemporaries so completely that D. S. Jordan (1905) was forced to complain: Wagner's theory of geographic speciation "is accepted as almost self-evident by every competent student of species or of the geographical distribution of species . . . but in the literature of evolu-

tion of the present day the principles set forth by Wagner have been almost universally ignored." The result was a tragic schism between experimentalists on one hand and naturalists on the other. Its ultimate bridging was made possible by the realization that most genetic changes are small and that mutations as such do not make new species. This cleared the way for a balanced treatment of the problem of geographic speciation by Rensch (1933), Dobzhansky (1937), Huxley (1942), and Mayr (1942).

THE MODERN SYNTHESIS

The development of the past ten or twenty years is characterized by the contribution from genetics of a firm foundation for the empirical findings of the naturalists of the preceding generation. The naturalists had discovered that isolation is necessary for speciation; the geneticists found out why. But one more step was necessary before this could be done successfully. The term and concept of isolation itself had to be re-examined. It turned out that it was applied to two entirely independent biological phenomena; just as in German the word *Entwicklungsgeschichte* is applied by some authors to ontogeny, by others to phylogeny. The two evolutionary meanings of isolation are geographic isolation and reproductive isolation. Both are equally important in the evolutionary process, but they play very different roles. *Geographic isolation* refers to the division of a gene pool in two by strictly extrinsic factors. It is a reversible phenomenon which in itself has no effect whatsoever on the two separated gene pools. However, it guarantees their independent development and permits the accumulation of an ever-increasing amount of genetic differences. *Reproductive isolation*, however, refers to what we might call the protective devices of a well-integrated and harmoniously coadapted gene pool against pollution by other gene pools. This is achieved by what Dobzhansky calls "isolating mechanisms," of which sterility is the best known but among higher animals by no means the most important. As soon as one clearly discriminates between the two kinds of isolation their respective roles at once become apparent. Geographic isolation is a necessity to permit the gradual building up of the genetic basis for the reproductive isolating mechanisms (polyploidy, as always, is an exception). To repeat once more: The genes within a gene pool form a harmonious whole which can evolve only as a whole. The first step then, in the multiplication of species, is a physical separation of a portion of the species, permitting it to go its own way genetically. What happens after this isolation depends on the genetic contents of the isolated population, on the totality of the selective forces working on it and on numerous chance phenomena (mutation, recombination, etc.). Divergence and the acquisition of isolating mechanisms in the separated gene pool may happen rapidly or may be delayed for millions of years. Speciation may be considered as essentially completed when the isolating mechanisms have reached that stage of perfection where the geographic isolation can be removed without resulting in genetic swamping of the new daughter species by the parental species.

In spite of essential agreement among evolutionists on the role of isolation, there is still divided opinion on a number of aspects of the isolation problem. Among these three may be singled out as perhaps occupying the greatest amount of attention in the recent literature:

(1) Are there as yet undiscovered forms of sympatric speciation? The search for proven cases of sympatric speciation, initiated by Darwin, still continues. I have myself reviewed the evidence *pro* and *con* in two recent summaries (Mayr, 1947, 1957*b*). It appears to me that this quest is becoming increasingly hopeless. The realization of the genetically highly complex nature of the isolating mechanisms and, more broadly speaking, of the intricate integration of the total gene pool of a population, makes it exceedingly difficult to conceive of a mechanism that would permit the building up of genetic isolating mechanisms within a physically undivided gene pool. The bridging effects of heterozygosity and the swamping effects of dispersal militate against the possibility of a lasting role of temporary conditioning.

(2) What role does selection play in the perfection of isolating mechanism? Two opposing theories can be found in the contemporary literature. According to one, isolating mechanisms are strictly an incidental by-product of the genetic changes occurring in geographically isolated populations and are perfected during this isolation without any *ad hoc* selection. According to the other, the development of isolating mechanisms is only started in isolation, but their perfection is achieved through natural selection after the incipient species has reestablished contact with the parental species.

It is not realized by most contemporary students

that this argument goes back to Darwin and Wallace. They used the term "sterility" where we would use the term "isolating mechanisms," but the essential part of the argument, the role of selection, has remained unchanged. Darwin first stated his views in *The Origin of Species* in the chapter on hybridism (1872: 320 ff.):

> At one time it appeared to me probable, as it has to others, that the sterility . . .[between species] might have been slowly acquired through the natural selection of slightly lessened degrees of fertility, which, like any other variation, spontaneously appeared in certain individuals of one variety when crossed with those of another variety. For it would clearly be advantageous to two varieties or incipient species, if they could be kept from blending. . . .

But, he continues, there are a number of facts known which do not fit with this hypothesis:

> In the first place, it may be remarked that species inhabiting distinct regions are often sterile when crossed; now it could clearly have been of no advantage to such separated species to have been rendered mutually sterile, and consequently this could not have been effected through natural selection; but it may perhaps be argued, that, if a species was rendered sterile with some one compatriot, sterility with other species would follow as a necessary contingency.

But, of course, this would not explain how it became sterile with this "compatriot." Darwin continues saying that the drastic differences so often observed between reciprocal crosses (e.g., ♂A × ♀B fertile, ♂B × ♀A sterile) is another phenomenon not explicable by selection, "for this peculiar state of the reproductive system could hardly have been advantageous in either species." He then continues:

> In considering the probability of natural selection having come into action, in rendering species mutually sterile, the greatest difficulty will be found to lie in the existence of many graduated steps from slightly lessened fertility to absolute sterility. It may be admitted that it would profit an incipient species, if it were rendered in some slight degree sterile when crossed with its parent form or with some other variety; for thus fewer bastardised and deteriorated offspring would be produced to commingle their blood with the new species in process of formation.

But Darwin is much too critical a thinker to be satisfied with a solution that is nothing but wishful thinking, and so he comes to the conclusion that such a scheme cannot operate (*op. cit.*, 321–322):

> But he who will take the trouble to reflect on the steps by which this first degree of sterility could be increased through natural selection to that high degree which is common with so many species . . . will find the subject extraordinarily complex. After mature reflection it seems to me that this could not have been effected through natural selection. Take the case of any two species which, when crossed produce few and sterile offspring; now, what is there which could favor the survival of those individuals which happened to be endowed in a slightly higher degree with mutual infertility, and which thus approached by one small step toward absolute sterility?

The same argument is presented, in part with identical phrases, in *The Variation of Animals and Plants Under Domestication* (1868). Here he states his conclusions even more unequivocally (p. 188):

> We may conclude that with animals the sterility of crossed species has not been slowly augmented through natural selection . . . . As species have not been rendered mutually infertile through the accumulative action of natural selection . . . we must infer that it has arisen incidentally during their slow formation in connection with other and unknown changes in their organisation,

a conclusion which is now quite generally accepted.

Wallace, on the other hand, was not willing to let natural selection take the back seat so completely. After having read what Darwin had stated in the 1868 work, he writes (in February, 1868, *More Letters* **1**: 288):

> I do not see your objection to sterility between allied species having been aided by Natural Selection. It appears to me that, given a differentiation of a species into two forms, each of which was adapted to a special sphere of existence, every slight degree of sterility would be a positive advantage, not to the individuals who were sterile, but to each form,

and continues to explain this in detail. This started an active exchange of letters (letters 209–214, *More Letters* **1**: 288–297) on the subject of the origin of sterility. Darwin, however, sticks by his guns:

> I feel sure that I am right about sterility and Natural Selection . . . . If sterility is caused or accumulated through Natural Selection, then, as every degree exists up to complete barrenness, Natural Selection must have the power of increasing it. Now take two species A and B, and assume that they are (by any means) half-sterile, *i.e.*, produce half the full number of offspring. Now try and make (by Natural Selection) A and B absolutely sterile when crossed, and you will find how difficult it is . . . .

This was a challenge to Wallace which he took up at once. He developed a most detailed thesis, consisting of nineteen propositions or theorems by which he thought he could do what Darwin considered impossible (March 1, 1868). In retrospect it is clear that Wallace made so many assumptions "to avoid complication," as he says, that he already starts out with virtually reproductively isolated species. Darwin's reaction is sufficiently amusing to be reproduced in full (March 17, *More Letters* **1**: 293):

> I do not feel that I shall grapple with the sterility argument till my return home; I have tried once or twice, and it has made my stomach feel as if it had been placed in a vice. Your paper has driven three of my children half mad—one sat up till 12 o'clock over it. My second son, the mathematician, thinks that you have omitted one almost inevitable deduction which apparently would modify the result. He has written out what he thinks, but I have not tried fully to understand him. I suppose that you do not care enough about the subject to like to see what he has written.

In this he misjudged Wallace, for only a week later Wallace writes (letter 212A): "I return your son's notes with my notes on them," and on goes the argument! Darwin's anguish is real (letter 213, p. 294):

> I have been considering the terrible problem. Let me first say that no man could have more earnestly wished for the success of Natural Selection in regard to sterility than I did, and when I considered a general statement (as in your last note) I always felt sure it would be worked out, but always failed in detail. The cause being, as I believe, that Natural Selection can not effect what is not good for the individual, including in this term a social community.

In the end Darwin apparently felt what he had said to Huxley a year earlier (*More Letters* **1**: 277): "Nature never made species mutually sterile by selection, nor will men." Wallace once more summarized his views in his *Darwinism*, 1889, p. 174–179. In retrospect it is clear that in spite of the brilliance of analysis on both sides, the problem at that time was an insoluble one, without an understanding of genetics, of population structure, and of the nature of all the other isolating mechanisms, in addition to sterility. It was though, while it lasted, a noble debate.

All the recent work indicates that by far the greatest part of the genetic basis of the isolating mechanisms is an incidental by-product of the genetic divergence of isolated gene pools and acquired during this isolation. There is no argument about this conclusion; indeed, it is obvious that there would be complete hybridization after the breakdown of geographic barriers if such isolating mechanism had not previously developed. The frequency of hybrid belts between formerly isolated portions of species fully substantiates this conclusion. The only remaining argument concerns one point: Will it lead to an improvement of the isolating mechanisms of the populations that are sympatric in the zone of overlap of two newly-formed species if an occasional hybrid is formed? Logically, the answer would have to be yes. Hybrids, at least in animals, are normally of decreased fitness as far as their contribution to the gene pool of the next generation is concerned. Since the fact of their occurrence indicates that the genetic isolating mechanisms of their parents were less than perfect, such hybridization should lead to an elimination of these less than perfect genes from the gene pool. Moore (1957) points out correctly that on the whole the effects of such selection will be confined to the zone of overlap. Furthermore, such a production of hybrids will strengthen the isolating mechanisms only if the hybrids are effectively sterile or inviable, because otherwise introgression between the two parental species would occur and, with it, an accelerating weakening of the reproductive isolation. Ecological and behavioral isolating mechanisms should be the ones most easily strengthened in such zones of overlap. This conclusion is supported by the available observational evidence, as cited by Dobzhansky (1951), which indicates an increased reproductive isolation between certain pairs of species in areas of geographical overlap. Lorković (1958) reports an additional case for the butterfly genus *Erebia* in the Alps.

(3) What is the effect of isolation on the genetic structure of populations? Virtually all work in genetics and animal breeding is done on completely isolated, closed populations. Geneticists have, on the whole, not been conscious of the fact that the conclusions at which they arrived on the basis of work on these closed populations are not necessarily equally true for the open populations of wild species. In a closed population the genetic input is restricted to a minimum, consisting of a few mutations; homozygosity is considerable and usually increasing, and the selective value of any gene is essentially constant. In open populations there is a high and (owing to immigration)

qualitatively variable genetic input, most loci (among those that are genetically variable within the species) are in the heterozygous state, and the selective value of a gene varies considerably with its genetic background (Mayr, 1954). The full consequences of the effects of the presence or absence of isolation on the genetic structure of gene pools have not yet been determined.

OTHER EVOLUTIONARY ASPECTS OF ISOLATION

The two most important evolutionary aspects of isolation are those we have discussed: geographic isolation in the process of the multiplication of species on the one hand, and reproductive isolation in the course of the origin of isolating mechanisms on the other. A third important aspect of isolation is its role in ecological interaction, particularly as determining degree and kind of competition. When an entire fauna or flora is isolated, as those of South America and Australia during the Tertiary, the effects of such isolation become apparent only when it breaks down. At a lower level, we find an isolation of associations and communities separated by ecological barriers and habitat preferences. No systematic treatment of the ecological consequences of presence or absence of such isolation is available nor will it be attempted here. It is mentioned mainly for the sake of completeness. On the whole, the effects of such isolation are self-evident and not controversial.

CONCLUSION

It will be evident from the above account that considerable clarification in our understanding of the evolutionary role of isolation has occurred during the last one hundred years. In the synthetic theory of evolution isolation plays its role in conjunction with natural selection, mutation, and other evolutionary factors rather than in competition with them as was believed by some of the founding fathers of the evolutionary theory. Indeed, it is the understanding of the genetic structure of populations which has finally provided the reasons for need for isolation during speciation which had long previously been established empirically.

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* Citations from Wagner and Weismann were translated by the author.

THE ROLE OF HYBRIDIZATION IN EVOLUTION

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INTRODUCTION

THE last quarter of the century which has elapsed since the publication of *The Origin of Species* has seen the gradual spread and almost universal acceptance by biologists actively working with problems of evolution of some form of the Neodarwinian concept of evolutionary dynamics. This concept may be broadly defined as one which, like Darwin's original concept, maintains that the direction and rate of evolution have been largely determined by natural selection. The role of selection however can be understood only in relation to all of the forces, both genetic and environmental, which act on a population at any stage of its evolution. Compared to Darwin's theory it incorporates a far better understanding of the genetic basis of variability in populations, acquired through applying Mendel's principles of particulate heredity to studies of changing gene frequencies.

According to the Neodarwinian theory, five processes stand out as the principal contributors to the action of selection. These are variation in the external environment, mutation (in the broadest sense, including chromosomal changes), genetic recombination, isolation, and the effects of chance variation in small populations. If we consider the role of hybridization in this context, we recognize it as a special case of genetic recombination. We must, however, have in mind a definition of hybridization which will carry the greatest possible meaning when this process is considered in relation to the other evolutionary processes. In view of the fact that the words "hybrid" and "hybridization" have been used for a great range of phenomena, from crosses between individuals differing with respect to a single gene to hybrids between distantly related species or even genera, the definition of hybridization most suitable to evolutionists requires a special discussion.

The most appropriate definition of hybridization for evolutionary purposes is one which recognizes that evolution goes on in space and time, and that the differentiation of populations depends largely on spatial isolation between them combined with a differential action of natural selection. When we recognize these facts, we realize that crossing between populations which have been previously isolated from each other for a long enough time to develop different adaptive norms will have profoundly different effects from crossing between two genetically different individuals belonging to the same population. This will be true regardless of whether or not reproductive isolation has developed between the populations, i.e., of whether the hybrid is sterile or fertile. I therefore propose an evolutionary definition of hybridization as follows: crossing between individuals belonging to separate populations which have different adaptive norms. This definition, of course, includes secondary intergradation, as defined by Mayr (1942), in addition to hybridization between reproductively isolated species.

One might object that this definition is hard to apply because in many actual situations the evolutionist has great difficulty in distinguishing between primary intergradation, which occurs when two segments of a population are diverging from each other while maintaining genetic connections, and secondary intergradation, which results from

later connections between previously isolated and adaptively differentiated populations. My answer to this objection is that one of the evolutionary facts of life consists in the sad realization that no hard and fast definitions can be made of general phenomena. If we wish to limit our concept of hybridization to crossing between species, then we are faced with the knotty problem of species definition. As has been clearly shown in a recent symposium (Mayr, 1957) this problem is by no means solved. The advantage of considering secondary intergradation along with interspecific hybridization is that both phenomena resemble each other in presenting to the environment, through segregation in later generations, a great variety of recombinations of the genetic differences which contribute to differential adaptation. Although the great majority of these recombinations are inadaptive, some of them may have superior adaptations, or may be especially well adapted to newly available ecological niches. Consequently, they can assume a major role in evolution. The extent to which this may be true forms the principal theme of the present discussion.

THE HISTORY OF KNOWLEDGE AND THEORIES ABOUT HYBRIDIZATION

Since remote antiquity, men have realized that animals and plants of different kinds can occasionally produce hybrid offspring, and in some instances, like the mule, this property of living things was put to human use even by prehistoric man. The scientific study of hybrids, however, began in the middle of the eighteenth century, when, through the stimulus of Linnaeus and his contemporaries, naturalists became generally aware of the distinctions between species. At that time sexual reproduction in higher plants was well understood, and these organisms, being easier to raise on a large scale, were used far more often than animals for controlled hybridizations. Linnaeus himself produced a well-known hybrid between two species of goats beard (*Tragopogon porrifolius* × *pratensis*); his observations have been fully confirmed in recent times by reproduction of this same hybrid. The fact that most interspecific hybrids are sterile was already widely recognized at this time.

The first systematic study of hybridization was made by Kölreuter from 1761 to 1806. He showed in a large number of examples that hybrids between plant species are usually intermediate between their parents, that most of them are sterile, and that the majority of the offspring which they do produce, usually from back crossing, tend to resemble one or the other of the parental species. At the end of the eighteenth century T. A. Knight in England was the first to use wide crossing between varieties or species on a large scale for breeding better varieties of cultivated plants. Kölreuter's work was extended during the middle of the nineteenth century by Gärtner, whose accomplishments, however, suffered from many errors and contradictions in their publication. In the latter part of the nineteenth century, C. Naudin, D. A. Godron, Max Wichura, and others continued to make hybrids, largely with the purpose of demonstrating either the validity or invalidity of hybrid sterility as a criterion of species. Meanwhile, starting in 1800 with the *Flora Britannica* of J. D. Smith, naturalists recorded an increasing number of spontaneous hybrids between wild species.

All of this exploratory work on plant hybridization was reviewed in a comprehensive monograph by Focke (1881). From his review, Focke reached the following significant conclusions, which are still valid. The ability of plant species to hybridize is widespread and general, but some groups are much more given to mixing in this fashion than others. For the most part, the ability for distantly related species to hybridize is a property of entire families, such as the willow (Salicaceae), rose (Rosaceae), and orchid families, but in other instances related genera differ in this respect. *Pelargonium* forms many hybrids, *Geranium* and *Erodium* very few. He suggested that plants with zygomorphic (irregular) flowers, like *Delphinium*, *Pelargonium*, and the orchids have a stronger tendency to hybridize than plants with actinomorphic or regular flowers; this tendency is still recognized, and is discussed in the present article. He also noted that in some genera certain particular species are notable for the large number of hybrid combinations which they can form. Focke had little to say about the offspring of hybrids other than that in some genera (*Salix*, *Pelargonium*, *Begonia*, *Calceolaria*) a succession of secondary hybridizations can result in combinations of as many as five or six species. In regard to natural hybrids, he made the important observation that they are most likely to occur where one of the parental species is relatively rare, or where the species bloom at sufficiently different seasons so that the first appearing flowers of the later species coincide with the height of flowering of the

earlier one. When both parental species are abundant and in full flower, the chances of interspecific pollination relative to pollination within the species are so low that hybrids are formed relatively infrequently.

Darwin, in his *Origin of Species,* discussed the problem of hybridization chiefly in connection with the distinctness of species, using the evidence of Kölreuter, Gärtner, and others to show that every transition can be found between fully fertile and completely sterile species hybrids. He also noted the fact that some species, as in *Nicotiana,* cross easily but produce completely sterile hybrids while others, like certain species of *Dianthus,* are very difficult to cross but the hybrids, when produced, are often fertile. Hence he reached the conclusion that the sterility of hybrids could not be used as an argument against the gradual evolution of one species from another. He went on to speculate as to how natural selection might bring about hybrid sterility barriers, but concluded that this subject was too complex for analysis, and wisely gave it up.

When Mendel's laws of heredity were rediscovered in 1900, a tremendous stimulus was given to the study of hybrids in all types of organisms, and particularly to the analysis of hybrid progeny. Since, however, Mendel emphasized the importance of crossing parents with few and easily definable differences from each other, early geneticists focussed their attention on crosses between closely related organisms with some degree of genetic purity, and either neglected the problem of crossing between more distantly related forms in nature, or assumed that this problem could be solved by a simple extension of Mendelian principles.

The first person to suggest that hybridization might play an important role in evolution was Lotsy (1916). His book is highly theoretical and speculative, and is supported by very few actual examples. He purposely avoided discussion of natural populations, since he felt that evolution could be understood only by focussing attention on genetically "pure" types, i.e., homozygotes. His theoretical concepts, particularly his peculiar redefinition of species and his development of a concept of heredity completely divorced from segregation, colored his work to such an extent that none of his conclusions can be accepted. His principal contribution was to point out that the complex segregation which results from a wide cross gives an extraordinarily rich material of genetic variability on which natural selection can operate. He also showed, with examples from the snapdragon (*Antirrhinum*), that recombination of genes can give types entirely different from either of the original parents.

Our modern understanding of the influence of hybridization on the course of evolution was ushered in by two series of investigations. First, the theoretical paper of Winge (1917) showed that by doubling their chromosome number, some interspecific hybrids in plants can give rise to fertile, true breeding amphiploid species, which are fully isolated from both of the parental species by barriers of hybrid incompatibility and sterility. Numerous experiments during the subsequent decade fully verified Winge's theory (Stebbins, 1950: chap. 8), and showed that in plants hybridization may often lead to the origin of new species. Of even broader significance was the series of studies of natural hybrid populations begun by Edgar Anderson (1936*a*; Anderson and Hubricht, 1938) about twenty-five years ago. His demonstration that the progeny of hybrids, particularly those which result from back crossing, may be favored by selection and thus contribute to evolutionary change within populations, ushered in our modern understanding of the role of hybridization in evolution. It has been the inspiration and keynote of much of the material presented here.

OCCURRENCE OF NATURAL HYBRIDIZATION

The role of hybridization, like that of any other single process affecting evolution, undoubtedly is far more important in some groups of organisms than in others. It must, therefore, be evaluated separately to at least some degree in different groups. To do this, we need to know as much as possible about the relative frequency at which natural hybrids occur in different groups of animals and plants.

Fortunately, data on natural hybrids are becoming more and more frequent, as evolutionists constantly add to the number of plant and animal groups subjected to intensive study. In many groups, particularly of higher plants, hybridization has been found to be far more common than was once suspected. Although it is less common in animals, it is not as rare as many zoologists have believed.

Data on non-vascular plants—algae, fungi, mosses, and liverworts—are still too scanty to evaluate. In the "Pteridophytes" or "vascular cryptogams" Manton, after an intensive cytological as

well as morphological study of European species, concludes (1950: 285) that "hybridization has been met with unexpectedly often and in a great variety of groups." Among North American ferns several workers, particularly Wagner (1951), have found a similar situation, and it is probably general throughout the group. Among the gymnosperms, hybrid conifers are well known. Natural occurrences have been described in *Pinus* by Papajoannon (1936), Zobel (1951), Moss (1949), and Mirov (1956), in *Abies* by Mattfeld (1930), and in *Juniperus* by Fassett (1945, etc.), Hall (1952), and Anderson (1953).

The list of natural hybrids among flowering plants or angiosperms grows larger with almost every issue of a botanical journal. Numerous examples have been cited elsewhere by the present author (Stebbins, 1950), where the fact was pointed out that certain woody groups, such as oaks (*Quercus*), willows (*Salix*), blueberries (*Vaccinium*), manzanitas (*Arctostaphylos*), *Ceanothus*, *Eucalyptus*, and *Acacia* are particularly prone to form natural hybrid swarms. In addition, "crystallized hybrid swarms," in the form of derived amphiploids and apomicts, are encountered in a large proportion of those groups which more erudite European botanists dignify with the epithet "botanicorum crux et scandalum" but which Americans are inclined to call just plain "messy." Examples are the hawthorns (*Crataegus*), blackberries (*Rubus*), and cinquefoils (*Potentilla*) in the Rosaceae, the pussy-paws (*Antennaria*), Arnicas, dandelions (*Taraxacum*) and hawkweeds (*Hieracium*) in the Compositae, and *Poa*, *Calamagrostis*, *Andropogon*, *Pennisetum*, and many other genera of grasses. The taxonomic difficulty, as well as the evolutionary success of these groups, is due largely to the after-effects of natural hybridization, which will be discussed later in this paper.

Occasional hybridization between recognizable species or subspecies is, therefore, the rule in flowering plants. In view of this fact, particular attention should be given to those groups in which hybridization is unexpectedly rare, in spite of the fact that related species often grow together in mixed colonies. One example is in the milkweed family (Asclepiadaceae) as discussed by Woodson (1941, 1954) and Holm (1950). Here the delimitation of genera is often difficult, but the species are well marked and constant, even though closely related species often grow together in mixed colonies, and are normally cross fertilizing. Hybrid swarms are unknown in this family. Another consists of various genera of the pea family (Leguminosae), particularly the peavines (*Lathyrus*), trefoils (*Lotus*), and clovers (*Trifolium*). In *Lathyrus*, Senn (1938) reported that artificial hybrids between species are very difficult to obtain. In *Lotus* and *Trifolium* the species native to California often grow side by side in mixed colonies, and even in the case of closely related species which have the same chromosome number, hybrids have never been seen, in spite of frequent searches for them.

Hybrids are far less common in animals than in plants, but are nevertheless known in many groups. Other than the arthropods, few invertebrate phyla have been investigated in this connection, and not many examples are known. Perhaps the best is the snail genus *Cerion* (Mayr and Rosen, 1956; Mayr, unpubl.), in which hybrid swarms similar to those found in plants are common on the islands of the Caribbean. Other examples are in the rotifer genera *Polyarthra* and *Conochilus* (Pejler, 1956).

Among arthropods the only example known to me outside of insects is in the small crustacean, *Daphnia* (Brooks, 1957). In insects natural hybrids and hybrid swarms are remarkably rare, considering the enormous number of species, and the fact that hundreds of artificial hybrids have been produced between species in various groups. In the fly genus *Drosophila*, which now has become the best known of any in regard to evolutionary genetics as well as from the standpoint of conventional Mendelian genetics, Patterson and Stone (1952) report 101 hybrid combinations produced in the laboratory, but only one example of a natural hybrid is known (*Mulleri* × *aldrichi*). This is because species which are closely enough related so that they can hybridize look so much alike that hybrids between them are usually difficult or impossible to recognize. Even considering this fact, however, one must admit that in relation to the number of species found in any one region, hybridization is far less common in *Drosophila* than in most plant genera, and probably rarer than in genera of vertebrates.

In other genera of flies (Diptera), such as the mosquitoes (*Culex*, Laven, 1953; *Anopheles*, Bates, 1939), hybrids between closely related species are rare, as in *Drosophila*. In most other orders of insects they are likewise rare, although certain European crickets (*Gryllus*, *Achaeta*), have long served as classic examples of species widely recognized by taxonomists which are never-

theless capable of forming hybrid swarms (Cousin, 1934; 1940; Cuénot, 1941). The most extensive records of natural hybridization among insects are, however, in the butterflies and moths, particularly the genera *Platysamia* (Sweadner, 1937), *Karanasa* (Avinoff and Sweadner, 1951), and *Colias* (Gerould, 1946; Hovanitz, 1953).

Among vertebrates, the fishes contain the largest proportion of recognized natural hybrids known in animals (Hubbs, 1955), these being particularly common in some groups of fresh-water fishes, such as the sunfishes (*Lepomis*), suckers (*Catastomus*), trout and salmon (*Salmo*), whitefish (*Coregonus*), and various tropical groups. The writer would like to remark in passing that he has often wondered whether fishes actually do hybridize more readily than other animals, or whether the larger number of well-documented examples is not due chiefly to the fact that a naturalist (Carl Hubbs) with a keen mind, an indefatigable energy, and a refreshing freedom from orthodoxy has chosen to investigate this subject with particular interest. Apparently, however, this tendency to hybridize does not extend to marine fishes, in which hybrids are generally rare.

Amphibia also contain groups in which hybrid swarms are common, particularly the toads (*Bufo*, Blair, 1941; Volpe, 1952; Cory and Manion, 1955). In frogs, on the other hand, natural hybrids are rare or lacking (Moore, 1949), and they are also apparently uncommon in salamanders (Spurway, 1953). Few data on reptiles are known to me, but the work of Kramer (1941) suggests that some hybridization may occur among lizards (*Lacerta*).

Birds are the best known taxonomically of all animals (Mayr, 1942). It is not surprising, therefore, that this class should provide the best-analyzed examples of secondary intergradation, or hybridization between previously isolated subspecies. In addition, occasional hybrids between well-recognized species occur in fifteen North American families (Cockrum, 1952), the ducks (Anatidae) alone containing twenty recorded examples.

In mammals, recorded examples of natural hybridization, even that between subspecies, or "secondary intergradation," are remarkably few. The scarcity of the latter phenomenon, however, may be due in part to the difficulty of distinguishing between primary and secondary intergradation (Hall, 1943; Blair, 1951). The best example known to me of natural hybrid swarms among wild mammals is in deer mice (*Peromyscus*, McCarley, 1954). There are, however, several examples of hybridization between domestic mammals and their wild relatives, such as dog × coyote (Dice, 1942; Hall, 1943*a*) and yak × cattle (Phillips, Tolstoy, and Johnson, 1946). These hybridizations, in most instances, have been made in attempts to produce breeds of the domestic species with particular adaptive properties.

Finally, since hybridization between races or subspecies comes under the scope of this review, we must recognize that this process has played a not insignificant role in at least the recent history of our own species. In a recent classification of the races of man, Coon, Garn, and Birdsell (1950) have recognized four out of thirty which are originating through hybridization begun in historical times. These are the Neo-Hawaiians, a mixture of Polynesian, Oriental, and European; the Ladino of Latin America; and the "colored" populations of the United States and South Africa. In addition, several other races, such as the Hindu, Hamite, and Polynesian, have in all probability been derived from mating in late prehistoric times between populations which were previously isolated from each other. Still earlier hybridization for which considerable evidence is now available is that between Neanderthal and Cro-Magnon or other races of modern man (Coon, 1954; Dobzhansky, 1955).

From this review, two obvious generalizations can be made. In the first place, hybridization between previously isolated populations of plants is frequent in nearly every group which has been studied, and, as will be brought out later, usually affects profoundly the course of evolution. In animals, on the other hand, the frequency of both hybridization and its significant after-effects appears to vary greatly from one group to another. Some genera, like *Cerion*, are much like plants in this respect, while in others, like *Drosophila*, hybridization appears to be so rare that a pronounced influence of this process on evolution is hard to imagine. Whether or not there is actually such a great difference in the amount of influence which hybridization has exerted in different groups of animals will be discussed below.

THE STERILITY OF INTERSPECIFIC HYBRIDS

The role of hybridization in evolution depends not on the frequency with which hybrids occur in nature, but on the effects that the hybrids which occur may have on genetic variability in natural

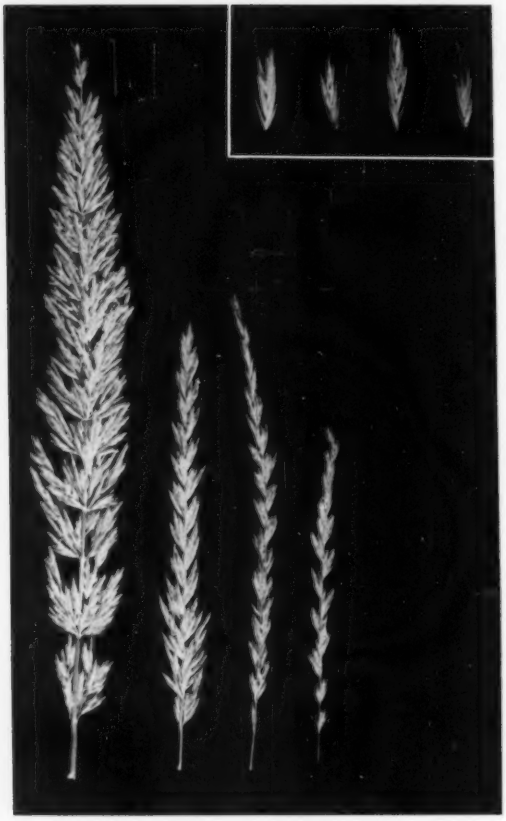

FIG. 1. Heads (× 2/5) and spikelets (× 1) of *Elymus triticoides* (left), *E. condensatus* (right), and their artificial and natural F_1 hybrids (middle).

populations. Until recently, there has been a widespread tendency to minimize such effects, on two grounds. First, the belief has been current that the high degree of sterility found in most interspecific hybrids prevents them from producing progeny which can affect significantly the trend of genetic variation. Secondly, Mendel's laws of inheritance, applied in their simpler forms to progenies segregating for a few well-marked differences, tell us that, even if a hybrid should produce offspring, these could do little more than reproduce either the parental types or an inconstant, segregating form similar to the F_1. The extensive studies of the last half century on species hybrids in plants have shown clearly that neither of these beliefs apply to them. The situation in animals is much less clear, but evidence is accumulating to suggest that at least some groups of animals are more like plants in these respects than has been hitherto suspected. The remainder of this article will be devoted largely to a review of the evidence which shows that, in spite of sterility and the tendency of the majority of segregates to resemble one or the other of their original parents, the progeny of interspecific and interracial hybrids may nevertheless affect profoundly the course of evolution. In organic evolution, as in many other affairs, both natural and human, the decisive influence is wielded not by the orthodox majority, but by a significant, progressive minority.

The first significant fact regarding hybrid sterility is its great variability. A slight reduction in fertility is known in many interracial hybrids within the same species, as in *Galeopsis*, *Campanula*, *Oenothera*, and many other genera (Stebbins, 1950: 257). From this condition all grades of sterility are frequent, down to percentages of fertility so low that they cannot be detected in the garden or laboratory, but can only be inferred from the behavior of natural populations. An example of this sort is found in the hybrid between two grass species of central California, beardless wild-rye (*Elymus triticoides*) and giant wild-rye or carrizo grass (*E. condensatus*). These two species, which are so distinct from each other that they can be distinguished at a glance even by a layman (fig. 1), hybridize readily, and the F_1 plants are vigorous and intermediate in appearance (Stebbins and Walters, 1949). Although both parents and the hybrid have the same chromosome number, $2n = 28$, the hybrids are extremely sterile. They form from 1 to 5 per cent of stainable pollen, but in spite of having cultivated them for several years in the presence of abundant normal pollen derived from their parents, we have never been able to find a single seed on them. In addition to artificial hybrids made from controlled pollinations, we have observed numerous wild plants which resemble closely the known hybrids, and which like them have a low degree of pollen fertility combined with almost complete failure of seed production. We must, however, infer that they occasionally produce seed, since intermediate clones are found which include a whole spectrum of variability from *E. triticoides* to *E. condensatus*, and these have likewise various grades of fertility. Furthermore, although these intermediates are most common in the region in which the two species overlap, they extend some distance beyond

the range of *E. condensatus*, particularly northeast of San Francisco Bay (fig. 2).

This situation can be understood when we consider the growth habit of the species concerned. *Elymus triticoides* is a sod grass, producing rhizomes much like those of the familiar weed, quack grass, and carries this property into its hybrids. A single hybrid clone, therefore, can exist for scores of years, and through rhizome production can spread over many square feet of ground, or even be transported mechanically to new sites. Thus, a single well-developed hybrid clone can bear each year as many as 1,000 flowering stems, each of which produces about 200 florets, making a total of 200,000 potential female gametophytes or eggs each year. If the seed fertility were as low as 0.001 per cent, or 1 seed per 100,000 florets, this would mean 2 seeds per year, or 200 seeds per F_1 clone, in the not improbable event that it should live for 100 years. Even if only 1 per cent of these seeds should produce viable offspring, the hybrid could not only maintain itself but even increase its numbers. Observation of various species of grasses in California has led me to conclude that situations like this are not uncommon in the family. Furthermore, plants with efficient mechanisms for vegetative reproduction are found in many other families, and in all such groups highly sterile hybrids might occasionally produce viable offspring.

A fact of perhaps even greater significance is that the offspring of many partly sterile hybrids are more fertile than the F_1, and this fertility often increases in later generations. The best-known way by which this is brought about is through chromosome doubling or amphiploidy, a special situation which will be treated in the next section. Fertility can also be increased by segregation, without change in the chromosome number, as has been demonstrated experimentally in several plant genera (Stebbins, 1950: 287). This is due to the fact that the initial sterility of F_1 hybrids is due to heterozygosity for certain particular sterility producing factors, either genic differences or chromosomal rearrangements. Segregates homozygous for these factors will have partly or completely restored fertility, even though they still exhibit intermediacy or recombinant conditions with respect to genetic differences not concerned with fertility.

Finally the fact must be emphasized that, since the sterility barriers between species always consist of a large number of genetic factors (Stebbins, 1958), homozygous recombinants for these factors

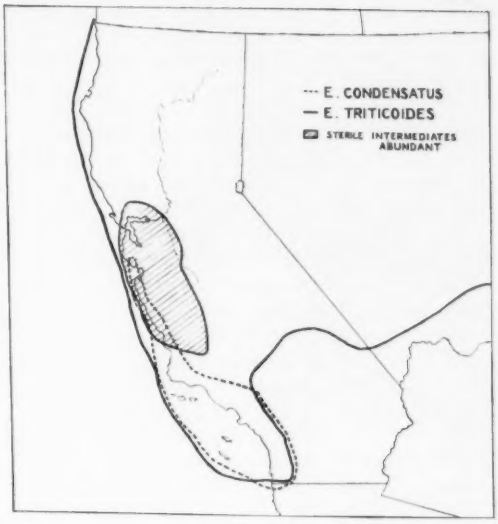

FIG. 2. Map showing the distribution in California of *Elymus triticoides*, *E. condensatus*, and sterile or partly fertile intermediate types.

can occur which are fully fertile, but which nevertheless form partly sterile hybrids when crossed to either of their original parents. In this way, segregation without change in chromosome number can lead to the formation of completely new species in the progeny of hybrids. Statistical computations presented elsewhere (Stebbins, 1957*a*) show that this can occur in a high percentage of such progeny, and a new "sibling species" in the genus *Elymus* has actually been produced in our laboratory in this manner (Stebbins, 1957*b*).

STABILIZATION OF HYBRID DERIVATIVES

These theoretical considerations lead inevitably to the conclusion that interspecific hybridization is not necessarily a "blind alley," which leads only to worthless sterile offspring or to restoration of the parental types, but that some hybrid derivatives are fertile, constant, stable, and genetically isolated from one or both of their original parents. This may, therefore, serve either to increase the adaptive variability present in one or both of the parental species, or they may form the nucleus of totally new species. The following are actual examples showing how this has come about.

Amphiploidy, or the production of stable, true-breeding new species through doubling the chromosome number of a sterile interspecific hy-

brid, is now generally recognized as one of the commonest ways in which plant species arise (Stebbins, 1950). The fact must be emphasized that a successful amphiploid species is an essentially permanent addition to the flora. It may migrate for hundreds or thousands of miles away from its origin and from the regions where its parental species occur. Furthermore, it may persist for geological ages, after one or both parental species have vanished from its place of origin; and several amphiploid species are known of which one or both parental diploid ancestors are extinct. Seven examples will serve to illustrate this point.

Two amphiploids which have originated during the past thirty years are those detected by Ownbey (1950) in goats beard (*Tragopogon*). Three European species of this genus (*T. porrifolius*, *T. pratensis*, and *T. dubius*), introduced into eastern Washington between 1910 and 1928, having hybridized to produce several F_1 plants, from which two different amphiploids, *T. dubius-porrifolius* and *T. dubius-pratensis*, have arisen. The natural colonies of these newly arisen species consisted of from 25 to 56 healthy self-reproducing individuals, occurring near railroad tracks and in vacant lots. These species are so young that their future is still problematical, but they are the first spontaneously arising species which have received scientific attention almost from their birth. Evolutionists can now report, a century after Darwin, that the actual origin of species has been observed in nature, and that the early evolution of newly arisen species can be followed in detail.

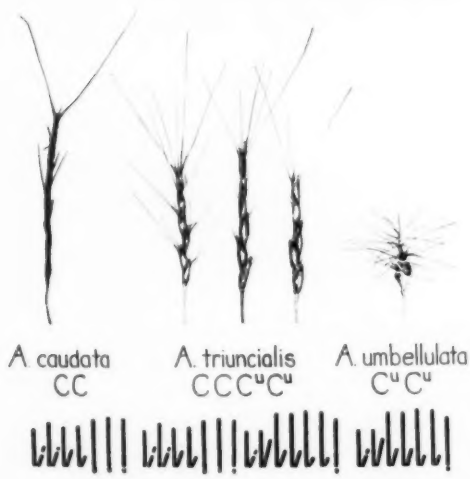

FIG. 3. Heads and chromosomes of three species of goat grass (*Aegilops*). At left, *A. caudata* ($2n = 14$); middle *A. triuncialis* var. *persica* ($2n = 28$); right *A. umbellulata* (from Kihara, 1954).

A second example is barb goat grass (*Aegilops triuncialis*), a common weed grass of the Mediterranean region, which has also become a troublesome introduction in parts of California. Kihara (1954) has shown that this species has acquired its 28 chromosomes by amphiploidy from two ancestral diploids, *A. caudata* and *A. umbellulata*, both of which have seven pairs of chromosomes (fig. 3). These two diploids are confined to the eastern Mediterranean region, where their ranges overlap over most of Asia Minor (fig. 4), so that hybridization between them and renewed formation of the amphiploid may still be occurring. *Aegilops triuncialis* is known only as a weed in environments created by man, either through cultivation or the grazing of domestic animals. In such habitats it has, nevertheless, spread all the way from Morocco in the southwest to Soviet Central Asia in the northeast, so that it occupies the entire province of Mediterranean agriculture. It is, furthermore, rather variable, having been divided into two subspecies and five varieties. From these facts the most logical conclusion is that *A. triuncialis* is no older than the dawn of agricultural and pastoral life, and is likewise not much younger. Its age, therefore, may be set at from 8,000 to 10,000 years.

A somewhat older amphiploid is the blue flag or iris (*I. versicolor*) of the eastern United States. This species, which has 108 chromosomes in its somatic cells, apparently originated from doubling the chromosome number of a hybrid between the Mississippi Valley blue flag (*I. virginica* var. *Shrevei*) and the Alaskan subspecies of the arctic iris (*I. setosa* var. *interior*) (Anderson, 1936*b*). At present, these two ancestral species are separated by a distance of more than 3,200 miles (5,400 km.), from Minnesota to central Alaska. Nevertheless, there is abundant fossil evidence to show that during the Pleistocene Ice Age species which are now confined to the arctic and subarctic regions occurred at lower latitudes, along the terminal moraine of the ice sheet. Furthermore, while the ice was retreating, the irregular terrain, containing massive soil-chilling blocks of ice side by side with outwash which must have been warmed by the sun's heat, was ideal for the sympatric occurrence of species adapted to very different climates. Under such conditions, the juxtaposition of the Mississippi and arctic irises

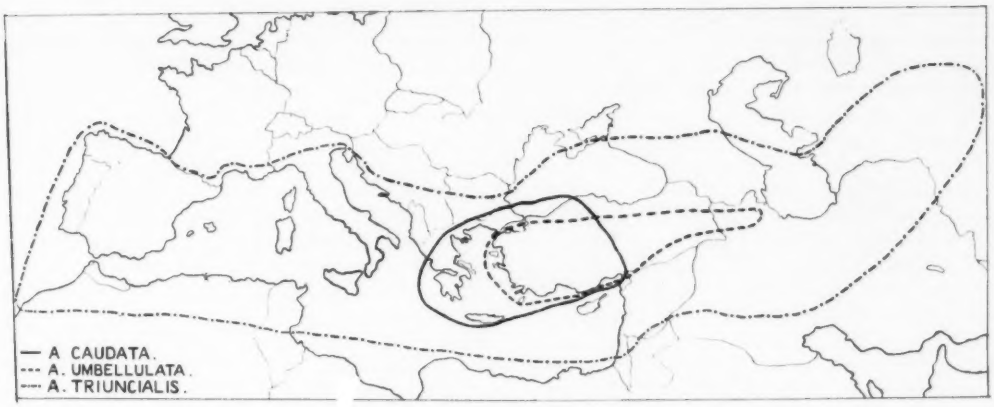

FIG. 4. Map showing the distribution of *Aegilops caudata, A. umbellulata,* and their amphiploid derivative *A. triuncialis.*

and their consequent hybridization is not hard to imagine, while at the same time new territory was being opened up by the retreating ice. This glaciated region is now the principal habitat of the amphiploid *I. versicolor.* A likely date for its origin is, therefore, the beginning of the retreat of the Wisconsin ice, about 25,000 years ago.

Still older is the California brome grass, *Bromus carinatus* (Stebbins 1947*a*), which on the basis of both phytogeographical and paleobotanical evidence is assumed to have arisen during the Pliocene epoch, from one million to five million years ago. The coast redwood of California (*Sequoia sempervirens*) is a probable relic amphiploid which is older yet. It has 66 chromosomes, which makes it hexaploid relative to the big tree (*Sequoiadendron giganteum*) and the dawn redwood (*Metasequoia glyptostroboides*), both of which have 22 chromosomes (Stebbins, 1948; Hirayoshi and Nakamura, 1943). Comparison of pollen and stomatal size between the living redwood and fossils of trees which lived in Japan during the Pliocene epoch shows that the two were identical in cell size, and presumably, therefore, in chromosome number (Miki and Hikita, 1951). On the other hand, fossil redwoods from Miocene and Oligocene deposits of Oregon, Montana, Colorado, and Poland have more slender branches and narrower leaves than the Pliocene or modern types, and although pollen and stomatal measurements are not available for them, these older fossils have the appearance of diploids. A reasonable guess, therefore, is that the hybridization and polyploidy which gave rise to the modern redwood took place in the Miocene epoch, from ten to twenty million years ago.

A sixth stage in the age of amphiploid species is, perhaps, represented by the New World cottons. The derivation of the tetraploid species of cotton of the New World (*Gossypium hirsutum, G. barbadense,* and *G. tomentosum*) from hybrids between a New World diploid related to the Peruvian *G. Raimondii* and an Old World species related to the African *G. herbaceum* is now known as certainly as any evolutionary event of the remote past can be, because of the large amount of cytogenetic evidence available to support this hypothesis (Hutchinson and Stephens, 1947; Gerstel, 1953). Although Hutchinson and Stephens have thought that these New World tetraploids originated through pre-Columbian migrations of man from Asia to America, bringing with them the already cultivated Old World diploids, this originally improbable hypothesis is made still more unlikely by Gerstel's discovery that chromosomally the Old World diploid ancestor of the New World tetraploids was most like the modern African *G. herbaceum* rather than the Asiatic *G. arboreum.* This lends further support to the writer's hypothesis (Stebbins, 1947), which assumes that the origin of the tetraploids took place in North America in the early part of the Tertiary period. Fossil evidence shows that woody elements of the flora which is now strictly of the Old World tropics existed at this time side by side with neotropical forms. If this hypothesis is correct, the age of the tetraploid cottons must be reckoned at from 40 million to 60 million

years. A similar age must probably be ascribed to a grass, *Heteropogon contortus*, which consists of a polyploid complex native to the tropics and subtropical regions of both the Old World and the New, the American forms consisting entirely of apomictic hexaploids (Emery and Brown, 1958).

The seventh and final stage in the age cycle of polyploids is represented by the two most primitive living vascular plants, *Psilotum* and *Tmesipteris* (Manton, 1950). In *Psilotum*, the lowest gametic chromosome number is $n = ca.$ 50, while in *Tmesipteris* it is about 100. Although no fossil record is available of these strange plants, their relationship to the Devonian Psilophytales is generally recognized. On this basis, as well as their isolated systematic position and occurrence in areas with an ancient flora like the Old World tropics and the Australasian region, the supposition that they are polyploids of which the original diploid ancestors flourished in the Paleozoic era, 200 million or more years ago, seems not unreasonable.

Polyploidy as a means of perpetuating hybrid derivatives in the form of new species is, as far as is known at present, confined to the plant kingdom and perhaps to a few apomictic forms of animals, such as earthworms and weevils (White, 1954). The absence of polyploidy in animals has long been recognized to be due in part to the fact that the *X-Y* mechanism of sex determination, which is the most common form in both arthropods and vertebrates, is severely upset by chromosome doubling, so that regular segregation of the sexes is impossible in such animals. As many authors have pointed out (Stebbins, 1950), this cannot be a complete explanation, since, in such genera of plants with separate sexes as willows (*Salix*), docks (*Rumex*), catchflies (*Melandrium*), and pussy toes (*Antennaria*), polyploid forms are well developed and have normal segregation of the sexes. This is apparently because in these plants the characters for maleness reside in the *Y* chromosome and are dominant, so that tetraploid plants of the *XXXY* constitution are full males, rather than intersexes, as they are in *Drosophila*. There is a strong likelihood that this type of sex determination exists in some fishes and amphibians (White, 1954), but it apparently has not permitted polyploidy to develop in them as it has in plants. I have suggested a reason for this fact elsewhere (Stebbins, 1958). A review of species hybrids in animals reveals the fact that their sterility is based chiefly upon the disharmonious action of genes in the development of the reproductive organs, rather than upon differences in chromosomal patterning, as is often true in plants. When hybrids with such genic sterility undergo chromosome doubling, their polyploid derivatives are as sterile as the original diploids, since the abnormal gene action is not counteracted. In short, the absence of amphiploid species in animals is due both to disturbances of the sex ratio and to the rarity or absence of chromosomal sterility as a limiting factor in species hybrids.

STABILIZATION BY INTROGRESSION

A completely different way by which the products of hybridization can become fixed and thus contribute to evolutionary change is the process first recognized by Edgar Anderson and named by him introgressive hybridization or introgression (Anderson, 1949; 1953). Three phases are essential to this process; the initial formation of F_1 hybrids, their back-crossing to one or the other of the parental species, and natural selection of certain recombinant types. In this way, populations of genotypes can become established which contain a few genes or chromosomal segments derived from one species on the genetic background of another. Although this result of hybridization is to be expected whenever two populations with different adaptive norms hybridize, it is likely to be the commonest outcome if the parental species are separated by well-developed barriers of reproductive isolation, and are cross-fertilizing. Under such circumstances, the relatively uncommon F_1 hybrids are much more likely to mate with members of the parental species than with each other, and the back-cross individuals derived from such matings are likewise more apt to be viable and fertile than are progeny from $F_1 \times F_1$ matings. Furthermore, in view of the complexity of the genetic mechanisms for adaptation possessed by species of higher plants and animals, new adaptations are much more likely to be developed by modifying the old ones, as happens with introgression, than by developing completely new gene combinations.

The fact must be emphasized that the products of introgression are permanent additions to the gene pool of the recurrent species. This is an inevitable result of the particulate nature of heredity, and of the action of selection, which forms the third phase of the introgression process. In genetic

terms, a simple example of introgression could be described as follows. Suppose that two species differ in respect to five gene loci, for which the alleles present in species I are designated *A*, *B*, *C*, *D*, and *E*, while those in species II are designated *a*, *b*, *c*, *d*, *e*. Recombination of these genes could rise to 32 different homozygous combinations, among which a typical introgressant from species II into species I would be *AABBccDDEE*. According to definition, the *cc* segment has been incorporated into the species I germ plasm because it confers a selective advantage under a particular environment, presumably a modification of the original environment of species I, into which the introgressants have entered. Under such circumstances, the relative permanence of genes, the homozygosity of the introgressed segment, and the action of natural selection would combine not only to retain the introgressive type, but also to foster its spread throughout the area occupied by the modified habitat to which it is adapted. We inevitably reach the conclusion, therefore, that introgressive genotypes not only persist indefinitely, but that also, like polyploids, they can migrate far beyond the areas in which they originated, and can actually survive after the non-introgressed parental species has become extinct.

Anderson (1953), recognizing this situation, has coined the term allopatric introgression for introgression between species which occupy different areas. He points out, furthermore, that this type of introgression is not only the most significant from the evolutionary standpoint, but also that it is the hardest for the naturalist to detect, since it requires familiarity with the genetic variation pattern in populations which are native to different areas, and "can often be intense without producing conspicuous results in any one area" (Anderson, 1953: 294). After reviewing, in company with various associates, the variation pattern in thirty genera of flowering plants in the central and eastern part of the United States, and correlating these patterns with the geological history of the region, Anderson has concluded that "all the readily detectable variation can be ascribed to introgression." This may be an exaggeration, but since most authors have tended to underestimate the importance of introgression in producing geographic races or subspecies, Anderson's conclusions, examples, and methods deserve careful attention from evolutionists.

The numerous examples of introgression now known in flowering plants have been so completely reviewed elsewhere (Anderson, 1949; 1953; Stebbins, 1950; Anderson and Stebbins, 1954), that they hardly need to be repeated here. I should like, however, to describe an additional example, which occurs in a different floristic area from other described examples, which involves two well-recognized genera, and in which both sympatric and allopatric introgression have been found. Bitter brush (*Purshia tridentata*) and cliff rose (*Cowania stansburiana*) are shrubs of the rose family common in parts of the Great Basin area of the western United States. Because of conspicuous differences in the number of carpels and the appearance of the fruits (fig. 5), they have always been regarded as well-marked genera, and although placed in the same tribe (Roseae or Dryadeae), they are usually separated rather widely in the system of this tribe. Hence the discovery on the part of several Utah botanists (Perry Plummer, Howard Stutz, Arthur Holmgren, W. S. Boyle), that probable hybrids between them are rather frequent, is rather surprising. These hybrids occur as solitary individuals in mixed stands of the parental species, and are intermediate in every respect. They have a somewhat reduced fertility. Both parental species and the hybrids have the somatic chromosome number 18.

Examining seedlings of *Purshia tridentata* all growing at the Great Basin Research Center, Ephraim, Utah, and derived from seeds collected in various parts of the range of the species, Mr. Plummer, Dr. Stutz, and the writer were im-

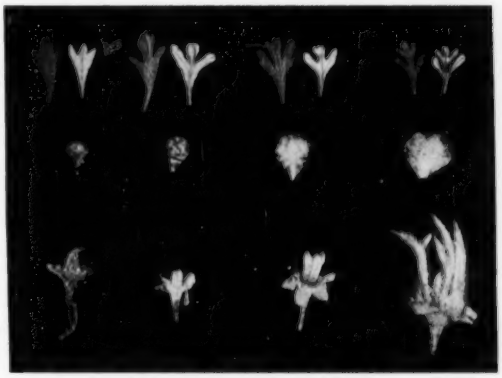

FIG. 5. Photograph of leaves, petals, and hypanthia with immature fruit of (left to right): *Purshia tridentata*, *Purshia tridentata* var. *glandulosa*, Natural F_1 hybrid, *P. tridentata* × *Cowania stansburiana*, from Ephraim Utah, and *C. stansburiana*.

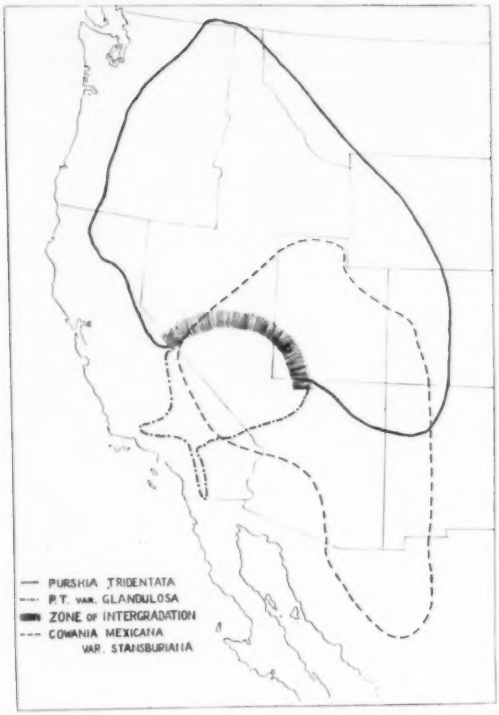

FIG. 6. Map showing the geographic distribution of *Purshia tridentata*, *P. tridentata* var. *glandulosa*, and *Cowania stansburiana*.

pressed with the fact that in the sum total of their vegetative characteristics the seedlings derived from Utah, within the range of *Cowania stansburiana*, were consistently more variable than those from areas to the north and west, and that this increased variability consisted entirely of the addition of characteristics found in *Cowania*. Later studies made by L. R. Thomas (unpubl.), using the methods of Anderson, have confirmed this feature in Utah populations of *P. tridentata* for reproductive as well as for vegetative characteristics. Sympatric introgression between *P. tridentata* and *C. stansburiana* is, therefore, widespread in the region of overlap.

Allopatric introgression between these two genera is exemplified by the populations classified as *Purshia glandulosa* Curran. This "species" is distinguished from *P. tridentata* by its leaves, which are bright green rather than grayish pubescent, possess conspicuous stalked glands on their margins, have narrower lobes, and are evergreen rather than deciduous; and by its petals, white rather than yellow. In all of these respects, *P. glandulosa* is simply *P. tridentata* with some characteristics of *C. stansburiana*. The distribution of *P. glandulosa* is south and west of *P. tridentata*, in southwestern Utah, southern Nevada, and southern California (fig. 6). This area is chiefly within the range of *C. stansburiana*, but the two species are not completely sympatric, since *P. glandulosa* usually occurs at higher altitudes. Since in their region of overlap in eastern California, *P. tridentata* and *P. glandulosa* form such extensive hybrid swarms that the identity of the parental types is completely obliterated, they are best regarded as subspecies of a single species.

The origin of *P. glandulosa* is best explained as follows. At the end of the Pleistocene pluvial period which corresponded with the ice age in the north, the mountain ranges of the southern Great Basin were still being uplifted, and a habitat was becoming available which combined a short growing season, due to the altitude, with excessive summer heat as well as aridity. Adaptation of *Purshia* to this new habitat was made possible by "borrowing" from *Cowania* through introgression gene combinations for greater tolerance of heat and aridity, along with certain distinctive morphological features. As these climatic conditions caused the introgressed types to replace the more typical *P. tridentata*, the former acquired through gene exchange and selection a uniformity of appearance which caused them to be recognized as a species.

The role of introgression is much more problematical in animals than in plants. Zoologists who have worked actively with species hybrids maintain that, as Hubbs (1955: 19) states: "it has been a factor of some significance in speciation." Clear-cut examples are, however, few in number. Hubbs has found that the numerous hybrids of sunfishes are usually sterile and sharply distinct from both parental species, but that in three places the hybrids graded into the parental species, so that gene exchange was suspected. In the whitefishes (*Coregonus*), the extensive studies of Svärdson, as reviewed by Brooks (1957), indicate that hybrids, although they undoubtedly occur, are very hard to distinguish from phenotypically modified individuals of the parental species, so that "the progeny from a backcross would probably be extremely difficult to detect in nature" (Brooks, 1957: 119).

Perhaps the best-documented examples of hy-

bridization followed by introgression in animals are those of the toads (*Bufo americanus* and *B. fowleri*), the towhees of Mexico (*Pipilo erythrophthalmus* and *P. ocai*), and the southwestern drosophilas of the *virilis* group. In the toads, A. P. Blair (1941) showed that the forest-inhabiting *B. americanus* and the plains species *B. fowleri* hybridize whenever their habitats come into contact with each other. The intermediacy of many individuals in respect to voice as well as form, and the artificial production of hybrids, supported his conclusions. Volpe (1952) showed that a population of toads from Westwood, New Jersey, agreed in both morphological and physiological characteristics with the variation pattern which would be expected on the assumption that *B. fowleri* had been introgressed with *B. americanus*. Finally, Cory and Manion (1955) showed that, as in plants, introgression in these toads is intimately associated with habitat differences. In a completely wooded area of northern Indiana, the toad population was found to consist entirely of pure *B. americanus;* in a pond twelve miles away surrounded by an open field, only typical *B. fowleri* was found, while a pond in the same area surrounded by mixed woods and fields contained an extensively hybridized and introgressed population.

In the outstanding work of Sibley (1950, 1954) on Mexican towhees the nature of the birds makes artificial hybridization or even direct observation of natural crossing very difficult, but the tremendous body of evidence available is very difficult to explain on any other basis than hybridization and introgression. The main facts are as follows. In the southeastern part of the Mexican highland, the spotted towhee (*Pipilo erythrophthalmus*) and collared towhee (*P. ocai*) occur together to some extent with either no intergradation, as in Oaxaca, or a small amount, as on Mount Orizaba. In western Mexico, typical *P. ocai* occurs by itself in the mountains of west central Jalisco, typical *P. erythrophthalmus* inhabits the entire Sierra Madre Occidental from Nayarit northward, while certain isolated summits rising from the Jaliscan plain (Cerro Viejo, Cerro de Tequila, Sierra de Ameca) contain hybrid swarms, in which most of the individuals combine in every possible way the characteristics of the parental species, and birds typical of either species are rare or absent. Finally, along the mountain chain extending from the vicinity of Mexico City of eastern Jalisco there occurs a character gradient or cline, from individuals typical of *P. erythrophthalmus* in the east to typical *P. ocai* in the west. These conclusions are based upon a careful analysis of five size differences and six color differences in a large series of populations.

Only two explanations of this situation are possible. One would be to assume that the intermediate populations of the central Mexican highland and of the isolated summits in Jalisco are a common ancestor from which the two species diverged. The other is that these populations are products of hybridization in recent times. The former explanation is ruled out partly by the great variability of the intermediate populations, which would be expected only on the assumption that they are heterozygous and segregating for widely divergent characteristics. Furthermore, the habitats of these intermediate areas are the most strongly disturbed by man in recent times, and so could hardly be expected to harbor ancient populations ancestral to a species like *P. erythrophthalmus*, which extends from Mexico northward throughout most of the United States, and even into Canada, and is divided into several subspecies. The explanation of hybridization and introgression fits best the facts of morphology, ecology, and genetic variability, as Sibley has pointed out.

The third example, that of *Drosophila texana, novamexicana,* and *americana,* of the *virilis* species group, is based on the cytogenetic analysis of Patterson and Stone (1952). Since the chromosomes of *D. americana,* in respect to both fusions and inversions, are a recombination of chromosomes found in *texana* and *novamexicana,* the hybrid origin of *americana* is most probable. Furthermore, the eastern strains of *americana* contain gene sequences more characteristic of *texana,* while the western *americana* strains are more like *novamexicana,* suggesting that the *americana* populations have been altered by hybridization and introgression since their inception. Hybridization between *texana* and *americana* is still occurring, so that this example is a borderline case between secondary intergradation and interspecific introgression.

Other examples of animal species in which introgression has been inferred from morphological data, but data on actual hybridization are lacking, are in the butterfly *Karanasa* (Avinoff and Sweadner, 1951), the woodpecker *Dendrocopos* (Miller, 1955), the rotifer genera *Polyarthra* and *Conochilus* (Pejler, 1956) and the "water

flea" *Daphnia* (Brooks, 1957). The reliability of strictly morphological data as criteria for introgression between animal species has been questioned by White and Key (1957), on the basis of their experience with Australian grasshoppers of the genus *Austroicetes*. Two closely related, sibling species of this genus appear to intergrade in one region, but cytological studies reveal a sharp discontinuity between them in chromosomal characteristics, for which all specimens are typical of one or the other species. From this evidence the absence of hybridization and introgression is inferred. This argumentation may be valid for their example, but to question the extensive evidence of Sibley on the basis of the situation in a completely different organism occurring on the other side of the world seems to this writer rather far fetched. Furthermore, sharp distinctness in cytological characteristics is not necessarily evidence that hybridization is impossible. In many different genera of plants, species with very different chromosomes hybridize readily and introgression between them occurs. Furthermore, if the chromosomal mechanisms of the parental species were partially incompatible with each other, one would expect natural selection to eliminate introgressants with intermediate chromosomal conditions, while retaining genotypes with chromosome behavior typical of one or the other parental species, but with new gene combinations.

The above evidence suggests that introgression may be much more widespread in animals than many zoologists have supposed. It indicates, furthermore, that conclusive evidence for introgression is much harder to obtain in animals than in plants. The acid test of reproducing the hybrids and introgressants artificially, which has now been accomplished in a large number of plant genera, is possible in only a relatively small number of animal groups, because of the difficulty of rearing most of them in captivity. Furthermore, the adaptive systems of animals are far more complex and precisely adjusted to their environment, so that selection permits fewer deviations from the adapted type. We might expect, therefore, that selection would act much more strongly on back-cross progeny from wide crossing, eliminating in a few generations all except those conforming either to one of the original adaptive types, or to some specific new adaptive combination. The variable hybrid swarms which are so common in plants, and which, through the use of Anderson's methods of character association and extrapolation, have yielded the best initial information for detecting introgression, are not likely to be tolerated by selection in most groups of animals. For this reason, evidence for introgression in animals may, perhaps, be best obtained by the method of synthesis. In those groups which are relatively easy to rear and hybridize, more experiments should be designed to study the effects of natural selection on back-cross progeny on a large scale and for many generations. The studies of Mettler (1957) on experimental populations of *Drosphila arizonensis* × *mojavensis* are a start in this direction. They show that in some derived populations the original parental type becomes reestablished, but that in others heterozygous introgressants become dominant in the population. In this connection the fact must be emphasized that when a population is developing a new adaptive system the decisive influence is exerted not by the mean viability or adaptiveness of all of the individuals produced, but by a few individuals, perhaps only a tiny fraction of the whole population, which happen to receive a particular new adaptive gene combination.

Finally, we must consider the similarity between certain after-effects of introgression and supposed mutation. Anderson (1953) pointed out that, if a chromosomal segment derived by introgression from another species is carried in the heterozygous condition with a homologous segment from the original species, it may become reduced in size by crossing over, down to a point where recombination via this process will occur only with extreme rarity. Such cross-overs can simulate mutations, both in the frequency at which they occur and in the fact that they will show typical Mendelian ratios when combined with the original, non-cross-over type. An actual example which fulfills all of the conditions of Anderson's model has been found by Mangelsdorf (1958) in strains of maize artificially introgressed with teosinte. On the basis of his evidence, coupled with both cytogenetic and archaeological evidence which indicates that hybridization and introgression between maize and teosinte have been going on for 1,600 years or more, Mangelsdorf has suggested that some of the more unusual examples of "mutation" recently uncovered in maize, particularly the activator-dissociation system of McClintock and the modulator system of Brink, may well be due to this residual crossing over of introgressed segments. If this is true, then the suggestion that introgres-

sion may have effects which go far beyond the time and place of the original hybridization carries tremendous weight.

STABILIZATION OF SEGREGATES FROM HYBRIDIZATION

Amphiploidy and introgression are the commonest ways in which the progeny of hybrids can become stabilized. Nevertheless, stabilization can occur without either of these processes. This is most likely to happen to the fertile progeny of mass hybridization between two subspecies, an event which will occur whenever changes in the earth's surface or climate permit two previously isolated and differentiated populations to come together. The fact to emphasize about such progeny is that segregation in them is very complex, owing to the large number of gene pairs which are segregating simultaneously. As a result, genotypes exactly like the original parents will be recovered rarely, and a tremendous number of new gene combinations will be presented to the environment, on which natural selection can act. Furthermore, as has been demonstrated experimentally in the progeny of artificial hybrids between subspecies of plants (Clausen and Hiesey, 1958), many of these new combinations will have completely new adaptive properties. A few individuals with the genetic property of transgressive variation, i.e., which in some characteristics exceed the limits of variation found in either of the parental types, can be expected to appear in the progeny of any wide cross between subspecies or species. Clausen and Hiesey have shown that among the progeny of a hybrid between *Potentilla glandulosa* subspecies *typica*, adapted to the coast of southern California, and *P. g.* subsp. *nevadensis*, adapted to alpine conditions in the Sierra Nevada, there occur genotypes which are better adapted to middle altitudes in the Sierra Nevada than is either parent, as well as others equally well adapted to coastal, mid-altitude, and subalpine habitats.

In the progeny of *Nicotiana alata* ("*Sanderae*") × *Langsdorffii*, Smith (1953) has shown that types with flowers larger than those of either parent can become fixed by selection. The transgression in this example is particularly significant, since the flowers of *N. alata* are among the largest in the genus. Smith's results suggest that flower size in *Nicotiana* could be increased above its present limits by recombination alone, without the occurrence of any new mutations.

Grant (1956) has found a remarkable example of transgression in an artificially produced amphiploid or doubled hybrid of *Gilia*. The number of parts of the flower—sepals, petals, and stamens, which in nearly all species of the Polemoniaceae is fixed at five, suddenly became extremely variable, both within the plants and from one plant to another. What is more remarkable, variants with an excess of the normal number of parts (6, 7, 8, or 9) appeared simultaneously with those having fewer (4, 3, or 2). Apparently once the intricate genetic balance present in the parental species became upset, a number of new types of interaction between genotype and environment were possible. In this connection Grant notes the significant fact that in *Leptodactylon*, one of the very few genera of the family possessing species with numbers of flower parts which deviate from five, one of these deviates has a higher and one a lower number of floral parts. Observations like these may eventually turn out to have a very great significance toward our understanding of the basis of major trends of evolution in the flowering plants.

Although comparable results are not available on the progeny of hybrids between natural subspecies or species of animals, Mather and Harrison (1949), starting with a cross between two inbred lines of *Drosophila*, were able to select for numbers of abdominal chaetae far exceeding those found in either parental line, and the relatively small sizes of the generations which they used precludes the possibility that many new mutations were involved. This suggests that natural selection in a radically new environment could likewise sort out transgressive variants from highly heterozygous populations, such as would result from crossing between races or subspecies.

The actual formation of new races or subspecies from segregates of interracial hybrids is usually hard to recognize because it requires a detailed knowledge of the recent evolutionary history of the group concerned. The writer has already mentioned two probable examples, one in *Potentilla glandulosa* of California, and one in the fir trees (*Abies*) of the Balkan region (Stebbins, 1950: 279–282). A third and even more striking example has been found by Tucker and Sauer (1958) in their study of the weedy amaranths (genus *Amaranthus*) of the Sacramento-San Joaquin delta region of central California.

Most examples of the origin of new types through segregation are at the level of races or subspecies, and so do not involve barriers of re-

productive isolation. Nevertheless, as has already been mentioned, segregation of the genetic factors responsible for reproductive isolation is certain to occur in any progeny derived from a partly fertile interspecific hybrid. Isolation of certain segregants from such progeny accompanied by selection for fertility can produce a population which possesses in addition to distinctive morphological and adaptive characteristics, a new balance of the factors promoting reproductive isolation. Consequently, such populations, by possessing some degree of reproductive isolation from both of their parental species, may form the beginning of an entirely new species.

Two examples of this sort are known to me. One is the "sibling species" of the *Elymus glaucus* complex produced artificially through crossing the woodland wild-rye (*E. glaucus*) with squirrel-tail grass (*Sitanion jubatum*, Stebbins, 1957). Since this production required one generation of back-crossing followed by selfing of the back-cross derivative, it is intermediate between simple segregation and introgression. The other example was produced by Drs. H. H. Smith and Kevin Daly from progeny of the hybrid between the two tobacco species, *Nicotiana alata* × *langsdorffii* (K. Daly, unpublished). From the partly sterile F_1 hybrid of this combination, three selections were made and carried through six generations of self-fertilization, one selected for large, one for intermediate, and one for small size of the flowers. When crossed with the parental species, the large flowered selection was completely interfertile with *N. alata* and partly intersterile with *N. langsdorffii*, and so could be regarded as *N. alata* introgressed with *N. langsdorffii*. The intermediate and small flowered selections, on the other hand, were completely interfertile with each other, and formed partly sterile hybrids when crossed with either of the parental species (fig. 7). Since they are recognizably different from both *N. alata* and *N. langsdorffii* in several different morphological characteristics, they could, with further isolation and selection, evolve into a new species.

The most suggestive evidence indicating that species have actually evolved from segregating progeny of hybrids is provided by the work of Straw (1955, 1956) on *Pentstemon*. He has shown that four species of this genus, *P. grinnellii*, *P. spectabilis*, *P. clevelandii*, and *P. centranthifolius*, occur sympatrically in southern California, and can form fertile hybrids through artificial cross-pollination in the garden. They are kept apart in nature, however, because their differences in floral structure and color adapt them to entirely different pollinators, these being respectively carpenter bees, wasps (*Pseudomaris*), solitary bees (Anthophoridae) and hummingbirds. Furthermore, *P. spectabilis* is in every way intermediate between the two-lipped, blue-flowered *P. grinnellii* and the tubular scarlet-flowered *P. centranthifolius*, closely resembling known hybrids between these two species. *Pentstemon clevelandii* bears a similar relationship to *P. spectabilis* and *P. centranthifolius*. The two intermediate types, *P. spectabilis* and *P. clevelandii*, are pioneers in chaparral and desert margin communities, at southern California, and so occupy relatively recent, still changing communities. Of the two extreme types, *P. grinnellii* occupies the more stable ponderosa pine forest community, while *P. centranthifolius* is by far the most widespread of the four, occurring in a variety of ecological situations. These extreme species are, therefore, probably older than the intermediate ones.

All of this evidence strongly supports the hypothesis of Straw, that *P. spectabilis* and *P. clevelandii* are both of hybrid origin, having been derived from hybrid swarms by the isolating and selective action of a new type of pollinator. The extensive hybridizations reported in *Pentstemon* by Viehmeyer (1958), show that the germ plasms of species belonging to six different sections can be combined either directly or via intermediary hybrids (i.e., the cross incompatible species *A* and *C* both exchange genes with species *B*). This evidence suggests that a large proportion of the more than 100 species of *Pentstemon* may have originated by hybridization in this manner.

The variation pattern in *Ophrys* of the Orchidaceae also consists of very distinct species which, nevertheless, occasionally form fully fertile hybrids (Stebbins and Ferlan, 1956). Since these flowers are also visited by highly specialized pollinators a similar mode of species origin appears likely. One is tempted to speculate that selection and isolation from hybrid swarms by specialized pollinators has likewise been responsible for the amazing speciation which has taken place in tropical orchids. In the best-known cultivated members of this family, the 50 or more species comprising the genera *Cattleya*, *Laelium*, and *Brassovala* can be combined to form a limitless array of diverse combinations. In view of this known genetic behavior, studies of natural populations of these species would be of particular interest.

The great similarity of speciation patterns in two large unrelated species groups which have in common their adaptation to specialized pollinators suggests that the high correlation between specialized mechanisms for cross pollination and proliferation of species is generally associated with the action of the pollinators in serving simultaneously as agents for natural selection and reproductive isolation. It is not, however, universally true that species of such genera cross easily to form fertile hybrids. In the milkweeds (*Asclepias*), for instance, hybridization even between closely related species is difficult or impossible (Woodson, 1954), while in the primroses (*Primula*) many of the species can be crossed, but the hybrids are highly sterile.

In the genus *Gilia* the taxonomic work and population studies of Grant (1953, 1956) suggest strongly that some of the diploid species are of hybrid origin. Although none of these has actually been reproduced artificially, enough hybridizations have been made with other species to suggest that the phylogeny proposed by him is a possible one. In this genus the origin of new types from segregation of hybrids, as postulated by Grant, involved both the segregation of chromosomal differences which promote hybrid sterility and differences in floral structure which promote specificity of insect pollination.

No comparable example of the segregation of morphological and adaptive differences simultaneously with genetic differences which contribute to reproductive isolation are known in animals. They should be sought, however, in species with highly specialized feeding habits, such as insects which feed on one or a few plant species and host specific parasites. In progeny of interracial or interspecific hybrids of such species, genotypes might be expected which could become quickly adapted to new feeding habits, which would simultaneously promote reproductive isolation and selection for a new adaptive complex of characters.

A possible example of animal species which have resulted from segregation from interspecific hybrids, accompanied by rigid selection for a new habitat, is provided by certain species of the leafhopper genus *Erythroneura*, described by Ross (1958). Detailed study of the morphological characteristics of more than 100 related species of this genus has made possible their arrangement into a series of phylogenetic lines, based on the degree and type of specialization of their genitalia. Four species, however, are anomalous in this scheme of classification, since they represent combinations of characteristics belonging to different phyletic lines. Ross explains this situation by assuming that these four anomalous species have been derived from hybrids between representatives of different phyletic lines, an explanation which apparently agrees best with his data.

In later generations progeny of the partly sterile hybrid between the stink bugs *Euschistus servus* × *variolarius* Sailer (1954 and unpubl.) has been able to isolate true breeding inbred lines which show a high degree of reproductive isolation from both of the parental species. This experiment suggests that the origin of species from interspecific hybrids can occur in insects, but the frequency with which this happens is at present entirely conjectural.

THE RELATION BETWEEN THE ENVIRONMENT AND THE OUTCOME OF HYBRIDIZATION

Enough has been said in the review of examples already presented to indicate that the outcome of hybridization depends very strongly upon the environment in which it takes place. This fact, first emphasized by Wiegand (1935), has become increasingly evident with each study of natural hybridization (Anderson, 1949; 1953; Stebbins, 1950; Anderson and Stebbins, 1954; Hubbs, 1955, etc.). From the numerous examples cited by these authors and in the present

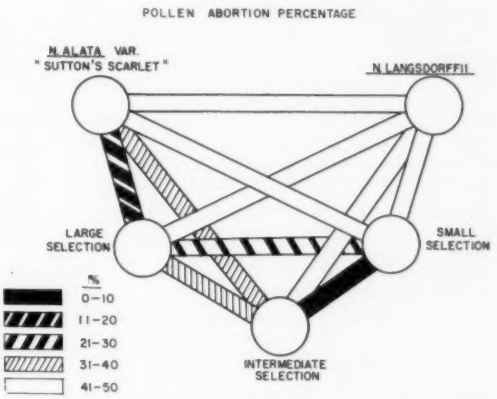

FIG. 7. Diagram showing the degree of pollen fertility in hybrids between *Nicotiana langsdorffii*, *N. alata* var. "Sutton's scarlet," and three corolla size selections. From K. Daly, thesis, Cornell University, 1957.

article the following generalization can be made. If two or more related species exist in a stable habitat to which all are well adapted, and if no unoccupied ecological niches are available, hybridization will be kept down to a minimum, and the few hybrids which are formed will have little or no effect on subsequent populations. If, on the other hand, the same species meet in an environment which is marginal for them, and particularly if the environment is changing in such a way that new ecological niches are being opened up, not only will the initial occurrences of hybridization be in many instances much more frequent, but also the selective action of the new environment will tend to increase certain hybrid derivatives, and so to build up new populations which have been more or less strongly influenced by hybridization. Furthermore, this action of selection on hybrid derivatives can in some instances continue for many generations after the initial crossing, and can be accompanied by their spread to regions far removed from the original site of hybridization.

Hubbs (1955) has added another biotic factor which affects the occurrence of hybridization in fishes. He has found that in waters which are poor in species, related species are likely to have relatively imperfectly developed mechanisms of reproductive isolation from each other, the breakdown of which leads to frequent hybridization. In regions with a rich fauna, on the other hand, mechanisms of reproductive isolation are much more strongly developed, and tend to prevent hybridization. He therefore reports the paradoxical situation that hybridization is frequent and the consequent variability of the species populations is high in regions with impoverished faunas such as the desert rivers of southeastern California and the postglacial lakes of the northeastern United States and Scandinavia, while in the rich and varied fauna of tropical coral reefs each species population is so well isolated from its relatives that hybridization is comparatively rare and the variability of each population in species differentiating characteristics is low.

Unfortunately, similar comparisons cannot be made between the impoverished terrestrial faunas or floras of northern or arid regions and the much richer biota of tropical rain forests. By analogy, however, we might expect that the latter regions, in spite of the larger number of species present, would have a lower proportion of hybrids and of puzzling, borderline cases between subspecies and species than would less favorable regions with more impoverished biota. If so, we should be forced to regard the rich biota of the equable tropical regions not as the scenes for the most active evolution of species, genera, and families, but principally as huge repositories for types which have to a large extent evolved in less favorable marginal areas, and have persisted in the great forests of the tropics because of the favorable conditions for existence which they offer.

A GENERAL HYPOTHESIS OF THE ROLE OF HYBRIDIZATION IN EVOLUTION

The material reviewed in the present article may be summarized by the following working hypothesis concerning the role of hybridization in evolution. Rates of evolution are recognized to be very variable, and exceptionally rapid rates tend to accompany the shift from one adaptive norm to another which is usually required for the major evolutionary advances (Simpson, 1953). The rate which prevails at any one time is a function of the genetic variability of the evolving population as it interacts with the prevailing environment. For the major advances to take place, therefore, a population with a high degree of genetic variability must be placed in an environment which is rapidly changing, and which offers to the population new ecological niches to which it can become adapted. Because of the slow rates at which it occurs, mutation can never provide by itself enough variability at any one time to fulfill such conditions. Genetic recombination must, therefore, be the major source of such variability, so that the evolutionary lines most likely to take advantage of a changing environment are those in which recombination is raised to a maximum. This is accomplished most effectively by mass hybridization between populations having different adaptive norms.

Although the short term effectiveness of such hybridization is limited by hybrid sterility and other effects of recombining the factors which contribute to reproductive isolation, these limitations can in many instances be overcome by polyploidy, introgression, or exceptional types of segregation. When this happens, the products of hybridization can form new evolutionary lines which are isolated from the ancestral types and are therefore free to evolve in new directions.

Although most examples of the successful outcome of hybridization result merely in types which combine in various ways the morphological

and adaptive characteristics of the parental forms, certain exceptional circumstances may enable the hybrid derivatives to transcend the range of variation found in their parents, and to generate truly new types. This can happen either through transgressive segregation, or through the establishment in the hybrid progeny of mutations which either existed in the parental species as inadaptive recessives, or which occurred during the hybridization process. These may have acquired a positive adaptive value in some new genetic recombinations resulting from hybridization.

This hypothesis can be put to the experimental test of both analysis and synthesis. If it is true, then the best examples of the origin of new species or genera should be found in regions where populations with a high degree of genetic variability are living in a variable, changing environment. Furthermore, synthesis of highly variable populations and their establishment in new, unoccupied environments should greatly speed up evolution, perhaps so much that major changes could be recognized within the lifetime of one observer. A century after Darwin, the field of experimental evolution which he founded is opening up ever widening vistas of thrilling research for the naturalist.

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VARIATION AND EVOLUTION

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(*Commemoration of the Centennial of the Publication of* The Origin of Species *by Charles Darwin, Annual Meeting of the American Philosophical Society, April, 1959*)

I

THE true greatness of a scientist may lie in the fact that his work carries the seeds of its own obsolescence. Darwin's theory of evolution is now one hundred years old. Commemoration of this centennial may easily be reduced to unctuous protestations about Darwin's having been so very right about so many things. His scientific intuition was, indeed, prodigious. But let us not forget that Darwin not only concludes the pre-Darwinian period of the development of biology, but also opens its post-Darwinian period.

The purpose of the present article is to review that portion of the evolutionary doctrine which was the veritable heel of Achilles of Darwin's theory, but which modern research has clarified to the extent of at least partly closing the breach. I mean, of course, the problem of the origin of hereditary variation. Darwin knew that individuals of the same species are never completely identical. The experience of animal and plant breeders bore witness that these individual differences are in part hereditary. Malthus stressed the fact that the number of children who survive must in the long run be smaller than the reproductive potential of the species. Darwin put these certitudes together and drew the necessary conclusion. The conclusion was natural selection.

Natural selection can, however, operate only if genetic variability is available. Of this Darwin was fully aware. I like to illustrate this point by an analogy. Natural selection manufactures new forms of life, adapted to new environments or improving the adaptation to old ones. Any manufacturing process uses some raw materials, the depletion of which brings the production to a halt. Heritable variation is the raw material with which natural selection works. Genetic variants are the building stones from which the genetic equipments of novel forms of life may be constructed. Johannsen's classical experiments in 1909 put a seal of finality to the conclusion that selection is ineffective when applied to a genetically uniform population. But where does the genetic variability come from? Darwin conceded that a solution of this problem eluded him. In his later years he grasped the reed of Lamarckian inheritance of acquired characters, which he had spurned earlier. This was a miscalculation. A solution of the riddle became possible only in our day. The raw materials of evolution arise through mutation.

There was still another difficulty, of the gravity of which Darwin was only dimly aware. Although he was familiar with what we now call Mendelian segregation, he, like everybody else in his time, accepted the "blood theory" of heredity, according to which the heredities of the parents are fused, or blended, in the child. In this he had, unluckily, no choice, as long as he overlooked the work of an obscure monk called Gregor Mendel. Now, if the parental heredities really became amalgamated in the child, then sexual reproduction would act as a destroyer of hereditary variability. This would aggravate the problem of the origin of variability severely; an explanation would have to be found not only for the origin but also for the maintenance of the hereditary variability in sexual populations, which we now call Mendelian populations. It is hard to avoid the thought that it was fortunate that Darwin did not perceive the insolubility of the puzzle in his day. For if he did, would we be celebrating the centennial of his work now? Darwin was not one to dodge a difficulty merely by using weasel words. It took more than half a century to discover that this was a spurious problem. Its spurious nature became fully apparent only when Chetverikov in 1926, and Fisher in 1930, realized the evolutionary implications of the earlier discoveries of Hardy (1908), Weinberg (1908), and Mendel (1865). Since the heredity is transmitted by genes, instead of by "blood," sexual reproduction perpetuates the hereditary variability instead of destroying it.[1]

[1] The work of Chetverikov was published in Russian and remained little known outside Russia. However, this is not a sufficient reason to ignore his contribution, as some authorities are doing.

II

Life is self-reproduction of complexly organized units from simple materials drawn from the environment. Heredity is implicit in self-reproduction. But absolutely accurate self-reproduction would make heritable variation, and hence evolution, impossible. The ultimate source of evolution must be the occasional breakdowns of heredity.

Genes may go on reproducing themselves accurately for a long time. However, mistakes in their reproduction do occur. The accuracy of the gene reproduction is often described, very misleadingly, as the gene remaining stable and unchanging for many years or even for centuries. What actually happens is that the gene interacts with the environment repeatedly, or even continuously, but the outcome of these interactions results in numerous copies of the same gene. A "mistake" in the gene reproduction means that the copy produced is not quite like the original. Two things may happen next. The altered gene may be unable to induce formation of its copies; if so, it is no longer a gene. If the new gene structure is copied successfully we have a mutant gene.

The above account is an oversimplification. Operationally, we are unable to specify what changes have occurred in a gene which has suffered a mutation. We infer that some changes may have happened, but what we actually observe are changes in the appearance or in functions in the organism which are transmissible from generation to generation. Perhaps the most general statement will be that we observe changes in what the organism does with its environment. When the process of gene copying takes a new path, the organism, which is a by-product of this process, is in some ways unlike its ancestors.

The trouble is, however, that we know at present several ways other than change in the gene structure, by which heritable changes in the organism may arise. The term "mutation" is in practice applied to a group of rather diverse phenomena—gene changes as well as various kinds of chromosomal aberrations. In all organisms except the simplest viruses, the genes are united in aggregates called chromosomes. Losses, reduplications, and internal reconstructions of the chromosomes and of their parts, all yield results which are not readily distinguishable from changes in the gene structure. The situation is certainly a complex one, and it is not made any less so by supposing (as some geneticists have done) that all mutations arise through repatterning of the chromosomes, and none are due to changes in the gene structure. It is true that the possibility that any given mutation may be due to a minute chromosome repatterning cannot be rigorously excluded, but it would be most astonishing if the genes themselves were completely unchangeable.

Other difficulties which the mutation concept has encountered are even more important for theories of evolution. Early in the current century, de Vries applied the term "mutation" to changes which he observed in his culture of the evening primrose, *Oenothera lamarckiana*. The genetic behavior of this plant is a very aberrant one; about three decades had to elapse before it was elucidated, chiefly by Cleland and his school. Most of the changes observed by de Vries would at present not be considered mutations at all. And yet these changes altered the appearance of the plants so much that de Vries believed his "mutants" to be new species. He attempted to draw a distinction between the minor or "fluctuating" variability within a species, and mutations which, he thought, yield new species by single large saltations. To many writers this seemed to portend the downfall of Darwinism.

Having the advantage of hindsight, we discern clearly why de Vries was led astray in this matter. Some botanists, his contemporaries, worked with the so-called elementary species or jordanones, which occur among plants that reproduce asexually or by self-pollination. These "elementary species" are clones or pure lines; the differences between them are, genetically, of about the same magnitude as those found among individuals of the same species, or even of the same race, in sexually reproducing organisms (Stebbins, 1950). It was unfortunate to confuse them with ordinary, or "Linnean," species in sexual forms. Linnean species arise through summation of many mutational steps and not by single mutations (except for the allopolyploids which need not concern us here). Modern evolution has revindicated Darwin's view, that there is no qualitative difference between the intra- and the interspecific variability.

The work of the Morgan school on mutations in *Drosophila* flies showed that most mutants appeared to be due to changes in single genes, although chromosomal aberrations were also discovered and studied in detail. The genes delimited as the units of mutability, of function, and of crossing over seemed to coincide, until exceptions were discovered by investigation of position effects, partial allelisms, and transductions. More-

over, mutants were shown to form a spectrum, starting with changes so drastic that they kill the early embryos, through "textbook mutants" with easily recognizable alterations of the external appearance of the fly, to mutants which only those with extensive practice or endowed with especially keen perception are able to apprehend, and finally to "modifiers" which are detected only by statistical techniques.

The school of Morgan used *Drosophila* mutants chiefly to study the architecture of the germ plasm, rather than problems of evolution. So were the mutants discovered in microorganisms used until recently to study problems mainly of chemical physiology. For these purposes, mutants sharp enough to be recognized and easily separated from other mutants and from the ancestral form were evidently preferable to those causing minute changes. "Good" mutants were preserved and "bad" ones discarded. It was inevitable that discrete, clear-cut, striking mutants came to be used as models for thinking about evolutionary problems as well. And yet this was not a reversion to de Vries's view that species arose by single mutations. In Morgan's classic *The Scientific Basis of Evolution* (1932), the word "species" is mentioned only in a footnote (p. 21); but the implication is clear throughout (see especially pp. 128–151) that evolution is due to occasional lucky mutants which happen to be useful rather than harmful. As one of Morgan's disciples, I held fairly similar views at that time, and they still continue to be held, explicitly or implicitly, by many geneticists. Their modern outgrowth is the rather widespread opinion that even quite remote organisms still carry many genes in common, and that the occurrence of similar enzymes and similar biochemical processes in such organisms is due to the retention of similar genes throughout the phylogeny (Green, 1955). This ignores the possibility that similar functions may be performed by genes descended from different ancestral genes.

III

The most logical, and also the easiest, way to study the raw materials from which evolutionary changes may arise is to explore the genetic variants which actually occur in natural populations of organisms. By about 1925, this matter was in a state of confusion. Geneticists were discovering, chiefly in *Drosophila*, more and more spectacular mutants; such mutants seemed, however, to be absent, or at least inordinately rare, in natural populations of these flies. In fact, *Drosophilae* found in nature appear to be rather less variable than many other insect species. H. F. Osborn and some others drew the conclusion that mutants are laboratory products which have no bearing on evolution.

A step toward a resolution of the contradiction was taken by Chetverikov in 1926. He pointed out that dominant mutants, if they are deleterious to their carriers, will be eliminated by natural selection more rapidly than the recessive ones, which will be carried in wild flies in heterozygous condition. He verified this inference by experiments in which he systematically inbred the progenies of *Drosophila melanogaster* flies collected in nature. Many of these flies were indeed heterozygous for recessive mutants; some mutants previously known only in laboratories were now discovered in natural populations as well. Timofeeff-Ressovsky, Dubinin, Ives, Spencer, Stone, and others confirmed Chetverikov's results and extended them to several other *Drosophila* species. In fact, every species so far tried has yielded concealed recessive mutants. The evidence for other organisms is more casual. Inbreeding strains of normally outbred species of animals and plants quite often yields some aberrant, abnormal, or defective individuals among the progenies. In some forms, such as certain species of pines, most of the progeny obtained by self-pollination consists of "rogues." In man the incidence of persons afflicted with recessive hereditary diseases and abnormalities is on the average greater in the offspring of cousin marriages than in the general population. This increased incidence of defects in families in which the parents are relatives is itself taken for presumptive evidence that a given defect is due to recessive mutant genes (Schull, 1958). Mutants do occur in natural populations of sexually reproducing organisms.

More sophisticated genetic methods are needed to detect concealed recessive lethal, semilethal, and subvital mutants which affect the viability without production of easily visible external changes in the body. A lethal is defined as a genetic variant which kills all of its carriers before the latter reach sexual maturity; a semilethal kills more than 50 per cent but fewer than 100 per cent of the carriers; and a subvital gene causes elimination of less than 50 per cent of its carriers. Following the lead of Dubinin and his collaborators (1934), these genetic methods were applied by other investigators to several species of *Drosophila*. The

TABLE 1

PERCENTAGES OF THE CHROMOSOMES IN NATURAL POPULATIONS OF CERTAIN SPECIES OF DROSOPHILA WHICH ARE LETHAL OR SEMILETHAL IN HOMOZYGOTES

Species	Chromosome	Percentage	Authority
melanogaster	Second	12.3–61.3	Dubinin *et al.*, Ives, Goldschmidt, etc.
willistoni	Second	28.4–41.2	Pavan *et al.*, Cordeiro, Townsend
willistoni	Third	25.6–32.8	Pavan *et al.*, Townsend
pseudoobscura	Second	21.3–33.0	Dobzhansky and Spassky
pseudoobscura	Third	25.0	Dobzhansky and Spassky
pseudoobscura	Fourth	25.9	Dobzhansky and Spassky
persimilis	Second	25.5	Dobzhansky and Spassky
persimilis	Third	22.7	Dobzhansky and Spassky
persimilis	Fourth	28.1	Dobzhansky and Spassky
prosaltans	Second	32.6	Cavalcanti, Dobzhansky, and Spassky
prosaltans	Third	9.5	Cavalcanti, Dobzhansky, and Spassky

results showed that lethal and other mutants occur far more frequently in natural populations of successful and in every way "normal" wild species than most geneticists were prepared to find. Some of the relevant data are summarized in table 1.

The meaning of the figures in table 1 needs clarification for non-geneticists. They show the percentages of chromosomes which contain genes for "hereditary diseases" that would kill the individuals who carry these chromosomes in double dose (i.e., who inherit them both from the mother and from the father). Thus, in a sample of *Drosophila pseudoobscura* flies from a certain locality in California, 33 per cent of the "second" chromosomes contained such genes and 67 per cent were free of them. The flies themselves were quite normal and vigorous, because the "hereditary diseases" in question were concealed in heterozygous condition. Now, every fly carries two "second" chromosomes, one of maternal and the other of paternal origin. Since a fraction 0.33 of the chromosomes in this population carried lethal genes, 0.33^2, or 10.89 per cent of flies had two such chromosomes; $0.33 \times 0.67 \times 2$, or 44.22 per cent, had one chromosome with a lethal and the other free of lethals; and 0.67^2, or 44.89 per cent, had two chromosomes without lethals. Similar calculations can be made also for chromosomes other than the "second" in the same population (the species carries five pairs of chromosomes). The result shows that only a minority of the flies were free of lethals in any chromosome, while a majority carried one to several lethals (those which carried two or more lethals were mostly viable and vigorous because the lethals in them were different, non-allelic, and each lethal was suppressed in the heterozygotes by the normal genes in the partner chromosome).

The chromosomes which are free of lethal or semilethal genes are by no means free of mutant genes of other kinds. Table 2 shows the frequency in natural populations of recessive genetic variants which make either the females or the males homozygous for them sterile. The sterile flies are often normal in appearance and in viability, they may have a normal sexual drive, and yet they fail to produce functional eggs or sperms. It is quite possible, although as far as I know not positively established, that sterility of some married couples in human populations is likewise genetically conditioned. In table 2 it can be seen that between 4 and 67 per cent of the chromosomes in different populations analyzed contained recessive "sterility genes." Note that the lowest frequencies of such genes are found again in *Drosophila prosaltans*, a species about which more will be said below. In other species, it can be calculated that only a minority of the flies in natural populations do not carry one or more concealed recessive genes for sterility.

Thus far we have concentrated our attention on the occurrence in nature of mutants with well-defined and even drastic effects, leading to death or sterility of their carriers. It is more difficult to obtain reliable data on the incidence of mutants with small effects, and yet it is probable that such minor mutants are far more important as raw materials of evolution than are the drastic mutants. (This statement does not imply that the small and the large mutants are discrete classes; all intermediates also occur.) In 1953, Wallace and Madden elaborated a statistical technique which permits estimation of the proportions of the chromosomes in natural populations which are

TABLE 2

PERCENTAGES OF THE CHROMOSOMES IN NATURAL POPULATIONS OF CERTAIN SPECIES OF DROSOPHILA WHICH CARRY RECESSIVE GENES FOR FEMALE OR FOR MALE STERILITY

Species	Chromosome	Percentage female sterility	Percentage male sterility	Authority
willistoni	Second	40.5	64.8	Pavan *et al.*
willistoni	Third	40.5	66.7	Pavan *et al.*
pseudoobscura	Second	10.6	8.3	Dobzhansky and Spassky
pseudoobscura	Third	13.6	10.5	Dobzhansky and Spassky
pseudoobscura	Fourth	4.3	11.8	Dobzhansky and Spassky
persimilis	Second	18.3	13.2	Dobzhansky and Spassky
persimilis	Third	14.3	15.7	Dobzhansky and Spassky
persimilis	Fourth	18.3	8.4	Dobzhansky and Spassky
prosaltans	Second	9.2	11.0	Dobzhansky and Spassky
prosaltans	Third	6.6	4.2	Dobzhansky and Spassky

TABLE 3

PERCENTAGE FREQUENCIES OF CHROMOSOMES WHICH ARE SUBVITAL IN HOMOZYGOUS CONDITION (AFTER DOBZHANSKY AND SPASSKY, 1953 AND 1954)

Species	Chromosome	Percentage
pseudoobscura	Second	93.5
pseudoobscura	Third	41.3
pseudoobscura	Fourth	95.4
persimilis	Second	84.4
persimilis	Third	74.2
persimilis	Fourth	98.4
prosaltans	Second	33.4
prosaltans	Third	14.5

subvital, i.e., cause rather mild constitutional weaknesses, in homozygous individuals. Such estimates can be at best only approximations, because the subvitality merges by imperceptible gradations into normality. The "normal" viability is, for the purpose of these studies, defined as the average viability possessed by flies in which the two chromosomes of each pair are taken at random from the population of a certain locality. In natural populations of the flies, as in human populations, outbreeding is the rule and inbreeding an exception. An individual may, then, be said to carry two specimens of each kind of gene, drawn at random from the gene pool of a given population.

The application of this technique to natural populations of *Drosophila* has yielded results rather astonishing even to those geneticists who became used to the great abundance of lethal and semilethal genetic variants in "normal" representatives of a species. As shown in table 3, in *Drosophila pseudoobscura* and *Drosophila persimilis* between 84 per cent and 99 per cent of the chromosomes are subvital in homozygous condition. Only in *Drosophila prosaltans* is the incidence of the subvital chromosomes somewhat lower. It should be noted that these figures apply to chromosomes free of lethals or semilethals, and thus must be understood as, in a sense, superimposed on the figures given in tables 1 and 2.

IV

The apparent rarity of mutants in nature impelled some biologists of a generation ago to reject the theory that the process of mutation is the fountainhead of evolutionary change. In recent years almost a surfeit of natural mutants has been discovered. True, nothing approaching exact quantitative data is available for organisms other than a few species of *Drosophila*. But only in these species have genetic tools needed for such work been devised. More indirect evidence, such as that derived from experiments on inbreeding, suggests that numerous recessive mutant genes are concealed in heterozygotes in populations of probably all sexual species, including man. This is also what one is led to expect on theoretical grounds, although, of course, the magnitude of the store of mutants may vary greatly in different species.

Modern evolutionary genetics must, then, face the problems of the structure, organization, and biological significance of the stores of mutants which natural populations are known to carry. One of the salient facts about these mutants is that most of them, like most mutants observed in laboratories, are deleterious to their carriers, at least when the mutants become homozygous. We find a great abundance of lethal, semilethal, sterile, and subvital mutants. The populations are said to carry *genetic loads* of deleterious variants. Only very rarely do we encounter a *Drosophila* chromosome which is supervital in double dose, i.e., which confers upon the homozygotes a vitality greater than the average in heterozygous individuals (which has been defined as "normal," see above).

Levene, Spassky, and the present writer (1955) have tested in a variety of experimental environments the performance of some homozygotes which were found to be supervital in one environment. Not one of the "supervital" homozygotes so tested maintained their supervitality throughout the range of environments to which they were exposed. In fact, when the environment was altered, the supervitality often turned into a decided subvitality. We are led to the conclusion that some homozygotes in *Drosophila* are "narrow specialists" which do extremely well in a certain narrow range of environments, but do not possess homeostasis, i.e., the capacity to adjust themselves to other environments. The capacity to respond homeostatically is, on the other hand, commonly found in heterozygotes which have the two chromosomes of each pair derived from parents who are usually not close relatives. Natural populations of *Drosophila* and of other sexual outbreeding forms consist mostly of such heterozygotes. This is, of course, one of the reasons why the "normal" viability is defined as stated above.

The dimensions of the genetic loads which natural populations carry can be fully revealed

only in genetic experiments which enforce homozygosis for all the chromosomes. In nature, the weight of the load crushes the carriers of the dominant defects, and the occasional recessive homozygotes which are produced even in panmictic populations. Hereditary diseases, defects, and weaknesses in human populations are manifestations of the genetic loads which these populations bear in their corporate genotypes. The question unavoidably presents itself, what maintains the genetic loads in existence? Why does natural selection, which was supposed already by Darwin to perpetuate the fit and to eliminate the unfit, fail to purge the deleterious mutants from natural populations? No fully satisfactory and universally agreed upon answers to these questions can yet be returned. This is a field which requires much further research. For the time being two working hypotheses are available, referred to as the classical hypothesis and the balance hypothesis respectively (Dobzhansky, 1955). It may as well be stated at the outset that these hypotheses are not mutually incompatible or exclusive; on the contrary, the problem may well be reduced to finding out what proportions of the genetic loads are maintained in different living species by the mechanisms visualized by these hypotheses.

The classical hypothesis is a direct descendant of Morgan's view referred to above, but its modern guise is due chiefly to H. J. Muller (1950 and later work). Its basic postulate is that almost all mutants that arise are unconditionally deleterious. Only rarely will a mutant fit better than the ancestral type in some ecological niche, and then it will outbreed and replace the original form of the species, at least in the niche for which it is suited. All other mutants are opposed by natural selection. Furthermore, Muller argues that few or no mutants are truly recessive, and that their effects in heterozygous condition are qualitatively similar to, although often much weaker than, in homozygotes. A mutant that is lethal or seriously incapacitating in homozygous condition may, then, produce a slight loss of fitness in heterozygotes. Even a slight loss of fitness will, however, be quite important. Rare mutants occur in outbreeding sexual populations, mostly in heterozygotes and only very rarely as homozygotes. Mutants of any one gene will usually be rare, even though mutants of all genes may in the aggregate add up to a very heavy mutational genetic load. Deleterious mutants will, then, cause slight incapacitations in many heterozygous individuals, as well as serious incapacitations or death of sporadic homozygotes. Muller argues that the sum total of the more covert harm done to the former may far outweigh the more overt harm to the latter.

The genetic loads found in natural populations of *Drosophila* are, from the standpoint of the classical hypothesis, mutational loads. They arise and are maintained because natural selection does not eliminate all mutants in the generation in which they appear. An interval of time spanning many generations may elapse between the origin and the weeding out of a harmful mutant, and during this interval the mutants are lurking in the gene pool doing harm to many heterozygous and homozygous individuals. Using certain assumptions, Muller has estimated that in human populations an average person is heterozygous for about seven deleterious genes. Morton, Crew, and Muller (1956) have refined this estimate to make it about four "lethal equivalents," i.e., a sum of deleterious effects in homozygous condition which is four times greater than necessary to reduce the fitness of a homozygote to zero. The mutational load tends to grow heavier if the mutation rates increase or if the selection rates decrease. Both contingencies seem to be realized in human populations—mutations are induced owing to misuse of x-rays and atomic energies, and selection slackens because modern medicine, technology, and philanthropy save and protect from elimination many genotypes which otherwise would have failed to be perpetuated. The mutational load in the human species is, therefore, increasing and the fitness decreasing.

V

Whether the classical hypothesis is capable of yielding a self-consistent picture of the genetic population structure may well be questioned. If the genetic load consists of unconditionally harmful mutants, then the fitness of a population will be promoted by making the load lighter. Even among the scanty data at our disposal there are some facts that do not readily fit in with this prediction. We have seen above that the genetic loads are lighter in *Drosophila prosaltans* than in other species (tables 1–3). Does this make *Drosophila prosaltans* a healthier and more successful species? Quite the contrary, *Drosophila prosaltans* turns out to be a rare and ecologically specialized form, while *Drosophila willistoni* and *Drosophila pseudoobscura* with which it is compared are

widespread, common, and ecologically versatile species.

If the genetic load which a population carries is merely an unavoidable evil, would, then, a man, or a *Drosophila*, completely free of the genetic variants which are deleterious in homozygous condition enjoy the greatest possible health, vigor and fitness? Would an ideally fit population be one consisting of such homozygously "normal" humans or of homozygously "normal" *Drosophilae*? We really do not know, since it is most doubtful that such populations ever existed in sexually reproducing and cross-fertilizing organisms. It may well be that the genetic loads were lighter in primitive human populations, or in those of our pre-human ancestors, than they are in modern man. But it is quite certain that the evolution of most of the living world has been enacted in sexual populations which carried genetic loads. The possibility must be considered that sexual species may have become adapted to their genetic loads, and even may have used these loads to some advantage. Such a possibility is visualized by the balance hypothesis of population structure.

Fisher pointed out in 1930 the interesting consequences of the situation when a heterozygote for two genetic variants has an adaptive value higher than in the two corresponding homozygotes. Suppose that the heterozygote A_1A_2 for two gene alleles or chromosomal structures A_1 and A_2 has a fitness 1, while the homozygotes, A_1A_1 and A_2A_2, have relative fitness $1 - s_1$, and $1 - s_2$, respectively. The values s_1 and s_2 are the selection coefficients, and the fractions $1 - s_1$ and $1 - s_2$ measure the relative reproductive efficiencies of the genotypes. Fisher showed that natural selection will, in an outbred sexual population, establish an equilibrium condition known as balanced polymorphism. Both genetic variants A_1 and A_2, will be preserved and will have predictable frequencies in the gene pool. Namely, A_1 will have the frequency $s_2/(s_1 + s_2)$, and A_2 the frequency $s_1/(s_1 + s_2)$. This will happen even if s_1, or s_2, or both, are equal to 1, i.e., if one or both genes are lethal when homozygous. We have an apparent paradox—natural selection will maintain in the population genetic variants which cause loss of fitness, disease, or even lethality in homozygotes, provided only that the heterozygotes possess hybrid vigor, or heterosis.

Spectacular cases of polymorphism have long been known in various species, particularly among insects, the populations of which consist of two or more classes of individuals sharply distinct in color patterns or other traits. Ford showed that these situations probably involve balanced polymorphisms. But the most complex systems of balanced polymorphisms have been found in species of *Drosophila*. Here they involve what would seem to be uncomfortably difficult traits—the gene orders in some chromosomes. The populations of many, though not of all, species of *Drosophila* are mixtures of two or more, up to forty-eight, freely interbreeding chromosomal forms, apparently identical in appearance but recognizable by examination of the giant chromosomes found in the cells of the larval salivary glands. Experiments showed that these elaborate polymorphic systems are balanced. Heterozygotes which carry two chromosomes of a pair with different gene orders are as a rule more fit in most environments than are the homozygotes with two chromosomes of the same pair similar in gene order (Dobzhansky, 1957, and earlier work).

The most important advantage of the chromosomal polymorphism in *Drosophila* for genetic studies lies in the fact that the fitness of the homo- and heterozygotes can be subjected to measurement in controlled experments. Such experiments have disclosed some interesting facts. Thus some of the homozygotes proved to be less than half as fit as the heterozygotes. These homozygotes may be said to be afflicted with semilethal hereditary diseases. And yet, they are permanent components of natural populations, and are maintained there by natural selection. Some exceptional populations of three species of *Drosophila* (*tropicalis, willistoni*, and *prosaltans*) have been studied by Pavan, da Cunha, Pavlovsky, and the writer. In these populations, appreciably more than 50 per cent of the individuals found in nature, and also of individuals in experimental populations set up in the laboratory, are heterozygotes for the same pair of chromosomal types. This situation can occur in a random-breeding population only if some of the progeny, who are homozygous for these chromosomes, are eliminated by death in each generation. The populations in which this happens may be suspected to be genetically degenerate and perhaps approaching extinction. But the evidence is otherwise—these populations are at least as vigorous as other populations of the same species in which the loss of homozygotes is smaller or absent. The loss of a part of the progeny is apparently compensated for by the heterosis in the surviving heterozygotes.

VI

Perhaps the key problem now facing the students of the genetic variability is to determine what share of the genetic loads in different forms of life can be attributed to the mutational and what to the balanced loads. This matter is important both for theory and for practice. A mutational load is kept up by recurrent mutation; a balanced load is maintained by the hybrid vigor in the heterozygotes. Stringent selection might diminish the mutational load; it would keep the balanced load at a fixed equilibrium level. Increased mutation rates, due to radiation to other causes, would increase the mutational loads. The reaction of a balanced load expected from increased mutation is a more complex matter; at least under some conditions the balanced load would be affected only slightly.

In man, there is at present but a single convincingly established case of balanced polymorphism, namely that of the sickle-cell gene in African populations. The homozygote for this gene usually dies of an acute anemia, but, as discovered by Allison, the heterozygote appears to be more resistant than is the "normal" homozygote to certain forms of malarial infections. However, I think that it is fair to say that there is presumptive evidence for several more balanced polymorphisms in man; there will doubtless be much activity in this field of study in the near future.

Lerner, who must be credited more than anyone else with the authorship of the balance hypothesis of population structure (1954, 1958), has summarized a large amount of evidence from his own experiments, and from those of other workers, dealing with selection for improved performance in breeds of domestic animals, particularly in poultry. What this evidence shows is essentially that top performance is very often found in heterozygotes. Attempts to fix this peak performance by rigid selection are unavailing, since when the selection is relaxed a relapse to a lower level of performance is observed. This resistance to continued gains with selection, and the loss of the gains already achieved upon relaxation of selection, Lerner has called the genetic homeostasis. A trait selected may show a high degree of heritability as estimated by usual methods, and yet no progress may be achieved by selection. The task of the breeder is, then, more intricate than the classical hypothesis has led us to believe. It is not isolation of some one genotype which engenders superior qualities in its carriers. It is rather construction of a new balanced gene pool of the population, such that the processes of Mendelian segregation and recombination would usually yield highly productive genotypes and phenotypes. The adaptive norm existing in a highly fit natural population, and that desired in a population under artificial selection, are aggregates of many genotypes in which the constituent alleles interact in a favorable manner.

Most impressive evidence in favor of the balance hypothesis has recently been obtained by Wallace (1957), and also by Burdick and Mukai (1958). Wallace used a collection of strains of *Drosophila melanogaster* homozygous for "second" chromosomes derived from certain experimental populations. Most of these homozygotes were subvital, i.e., had viabilities lower than in outbred heterozygous flies. By means of an ingenious experimental procedure, Wallace compared the viabilities of these homozygotes with those of similar flies which had one of their "second" chromosomes inherited from an ancestor irradiated with a small (for a fly) amount of x-rays. The irradiation had presumably induced some mutations, so that the flies which carried the irradiated chromosomes were now heterozygous for the induced mutants. The flies with the irradiated chromosomes proved to be slightly, but statistically significantly, more viable than the homozygous flies. Several quite rigorous tests imposed on the data have upheld the reality of this astonishing result.

Wallace's findings are especially impressive since heterozygosis for lethal mutants is known to be, on the average, deleterious. This has been demonstrated by Stern *et al.*(1952) for radiation-induced and for spontaneous lethals in *Drosophila melanogaster*, and by Cordeiro (1952) and Prout (1952) for lethals found in natural population of *Drosophila willistoni*. The conclusion is inescapable that mutants which stop short of lethality when homozygous may, on the average, be heterotic when heterozygous. It remains to be determined by future experiments whether irradiation of one chromosome set in a normal outbred fly will also have an average heterotic effect. Be that as it may, it can no longer be doubted that many mutants which are deleterious when homozygous tend, at least under certain conditions, to act as viability stimulants when heterozygous. This contravenes one of the fundamental assumptions of the classical hypothesis of population structure.

VII

The source of the genetic variability present in living populations is ultimately mutation. Sexual reproduction does not destroy, it preserves variability. To this extent, the fundamental problem posed by Darwin has been solved, and its solution may fairly be regarded an important step toward a satisfactory theory of evolution. But as so often happens in science, the solution of a problem has raised new issues which seem more intractable. Some of these issues have been stated by the classical and the balance hypotheses of population structure. We may now attempt to indicate the broad lines of these issues as viewed from another angle.

This concerns the role of the gene recombination in the production of the genetic variability. According to the second law of Mendel, n unfixed genes represented in a population by only two alleles each, may yield 3^n genotypes, 2^n of which will be homozygotes. The debatable point is, what role this shuffling of genes plays in the production of the adaptive norm of a species or a population. The adaptive norm comprises the representatives of a species or a population which are able to survive and to reproduce successfully in the environments in which the species usually occurs. In this sense, "normal" men or "normal" *Drosophilae* make up a great bulk of the respective populations. The adaptive norm may be contrasted with a residue consisting of carriers of hereditary defects and diseases. Now, the classical and the balance hypotheses suggest different models to describe the constitution of the adaptive norm.

The classical model assumes that the "normal" or "wild-type" representatives of a species or a race are (except in obviously polymorphic species) uniform and homozygous for most "normal" genes. The genetic variability present in populations is, according to this model, caused by harmful mutants not yet eliminated by natural selection, and by genetic variants which are, at least temporarily, indifferent to the welfare of the organism. The variability of the human facial features has been used as an example of such neutral variability. The balance hypothesis suggests another model: The adaptive norm is an array of numerous genotypes. Since the carriers of these genotypes interbreed freely, all, or at least a great majority, of the individuals in a Mendelian population are multiply heterozygous.

Spiess, Spassky, Levene, and the writer (in press) have attempted to put this matter to experimental test. We have chosen three species—*Drosophila pseudoobscura, D. persimilis,* and *D. prosaltans*; in each species we took a sample of 20 chromosomes, extracted equally from natural populations of each of two different localities. Tables 1 and 3 show that most "natural" chromosomes are more or less deleterious to their carriers when in homozygous condition. We rejected chromosomes which were lethal, semilethal, or plainly subvital to homozygotes, and deliberately selected chromosomes which yielded uniformly normal to mildly subvital homozygotes. The strains carrying these chromosomes were then intercrossed in all possible combinations—with 20 chromosomes 190 different intercrosses are evidently possible. Females carrying pairs of these chromosomes (i.e., heterozygous for two chromosomes each) were then crossed to males with suitable mutant marker genes. From the progeny of each intercross 10 males were then taken, 1,900 males in all. Every one of them carried one chromosome with the gene marker, and one chromosome which represented a product of recombination of parts of the two "natural" chromosomes which were carried in its mother. By means of a special genetic technique (referred to also on page 254) the viability of these recombined chromosomes in homozygous condition was examined.

An extraordinary variability was observed among the recombination products. Remember that the original chromosomes were pretty much alike and yielded fairly normally viable homozygotes. Among the recombination chromosomes the viability varied all the way from normality to complete lethality. Lethal hereditary diseases, so-called synthetic lethals, can thus arise through recombination of the gene contents in chromosomes which seem to contain only "healthy" genes. Synthetic lethals are, however, merely the most spectacular recombination products. More important is to discover how great is the total mass of variability released in these experiments by the recombination process. The statistical method suitable for this purpose is calculation of the variance observed among the recombination chromosomes. The magnitude of the variances in the three species investigated is shown in table 4.

The numbers in table 4 require an explanation. In *Drosophila pseudoobscura*, a single generation of gene recombination among pairs of chromo-

somes which are ostensibly alike in their effects recreates, astonishingly enough, as much as 43 per cent of the total variance present in the natural populations from which these chromosomes were derived. In *Drosophila persimilis* and *Drosophila prosaltans*, the percentages are not quite so high, but still amount to 24–25 per cent. In other words, the shuffling of the genes stored in only two chromosomes, and these definitely selected to be uniform in their effects, can yield a substantial proportion of the total genetic variance present in natural populations.

Some details of these results are worth noting. The viability of a recombination product is determined by the specific properties of the genes it contains. Therefore, a chromosome A may give highly viable recombination products with a chromosome B, and B with C, but the recombination of A and C may yield poorly viable, and even lethal, products. Similarly, the recombination products of A with B, and B with C, may be rather uniform, but A with C may yield a high variance. Finally, it is possible to show that much of the variance obtained among the recombination products is due to so-called epistatic interactions between the genes, and only a minor part to simple additive gene effects.

TABLE 4

VARIANCE OF THE VIABILITY EFFECTS IN HOMOZYGOUS CONDITION OBSERVED AMONG THE CHROMOSOMES FOUND IN NATURAL POPULATIONS OF DROSOPHILA, AND AMONG THE CHROMOSOMES OBTAINED BY RECOMBINATION IN THE EXPERIMENTS DESCRIBED IN THE TEXT

Species	A. Natural chromosomes	B. Experimental chromosomes	Percentage 100B/A
pseudoobscura	140	60	43
persimilis	110	26	24
prosaltans	200	50	25

VIII

The conclusion seems warranted that, in species with a genetic structure like the *Drosophilae* which we have studied, the genetic variability in natural populations is kept up mainly by the recombination of the genetic variants stored in the gene pool. These gene variants have arisen ultimately by mutation. Nevertheless, so great is their accumulated store that a suppression of the mutation process, if it were attainable, would not appreciably diminish the genetic variability available for evolutionary adaptations, and this probably for many generations.

It is not due to academic scruples alone that the above conclusion is explicitly limited to the species actually studied. For one of the tenets of modern evolutionary thought is that there are many evolutionary patterns rather than a single universal one. This does not mean that we are losing sight of the fundamental unity of the living world. Mutation and selection are components of probably all evolutionary histories. But recognition of the unity is compatible with acknowledgment of the variety. Compare sexually reproducing organisms with those which are predominantly or exclusively asexual. In the former, a virtually unlimited diversity of genotypes can arise through Mendelian recombination; in the latter, the variability is restricted to what can result from the occurrence of different mutants in different lines of descent. Consider, on the one hand, the higher forms of life in which the haplophase has only a brief existence, and, on the other hand, the lower forms in which meiosis occurs immediately following the fertilization. The predominantly diploid forms will carry much greater mutational loads than the haploid ones, but the former will be able to exploit the advantages of heterosis accruing from the possession of balanced loads.

Consider finally the microorganisms in which billions of individuals arise in a matter of hours or days from a single cell; by contrast, in the populations of some higher forms, such as mammals or trees, an individual may live for years, decades, or even centuries, and the breeding population cannot grow very rapidly. In the former an individual does not count for much. Microorganisms seem to rely upon the occurrence of an appropriate mutation where and when need to supply the genetic materials for adaptive modification. They can withstand destruction of innumerable individuals by environmental changes, provided only that a single mutant cell will be available to found a new colony adapted to the new environment. Among higher organisms, the destruction of a majority of members of a population may mean the extinction of the colony, the race, or the species. Not only populations but also individuals of higher organisms must be adaptable to changing environments. Therefore, the genetic adaptation in the evolutionary process is most effective in higher organisms when it makes the individual most adaptable. Increasing

"wisdom of the body," i.e., gradual improvement of physiological and developmental homeostatic mechanisms, is, hence, among the chief criteria of progressive evolution.

In no way inconsistent with the acknowledgment of the existence of a variety of evolutionary patterns in different living forms is the recognition of broad similarities between some of them. Consider the sexually reproducing, diploid, outbreeding animal species. In such species, from *Drosophila* to man, enforced inbreeding results in a lowering of the average fitness. The experimental evidence, most conclusive in *Drosophila*, more fragmentary but concordant in other forms, suggests that "normal" individuals of such species are all multiply heterozygous. Lerner (1954) has advanced the very interesting idea, that the maintenance of the adaptedness in these forms may depend upon the preservation of a certain obligate level of heterozygosity. Inbreeding lowers this level, and the decrease of the fitness may be ascribed to this fact rather than to homozygosis for specific deleterious recessive mutant genes. Crossing the inbred lines, on the contrary, increases the level of the heterozygosity and consequently increases the fitness.

Haldane and others have adduced biochemical arguments in favor of the view that heterosis may be a consequence of heterozygosity *per se*. This is a matter for further study; for the time being the assumption that there is an intrinsic advantage simply in being heterozygous has only a standing of an unproven working hypothesis. But, as pointed out on page 258, it is certain that outbreeding sexual diploid species have evolved for countless generations as Mendelian populations in which certain levels of heterozygosity were being maintained. It is this heterozygous state that has been acted upon, and gradually perfected by natural selection. The improved viability of *Drosophila* heterozygous for new mutational changes induced by x-rays in the experiments of Wallace (see page 259) may also be regarded as due to a restoration of the normal level of heterozygosity established in the process of evolution. Lerner's idea helps to make sense of what otherwise is a congeries of disconnected data.

We may repeat today the admission made by Darwin a century ago: "Our ignorance of the laws of variation is profound." But the century has not been wasted, since modern biology possesses methods and tools with which to study these laws.

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THE NATURE OF THE FOSSIL RECORD

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INTRODUCTION

THE past two decades have witnessed a remarkable revival of interest in organic evolution and the emergence of a broad new discipline, the study of evolution, which integrates and synthesizes evidence derived from systematic biology, genetics, and paleontology. In the resulting rapid growth of knowledge of evolution, paleontology has played a leading role far beyond that envisioned by Darwin of supplying proofs that evolution has, indeed, occurred. Broadly defined, paleontology is the *geological history of life*, and as such it is vast in scope, and diffuse. In spite of the fact that the number of dedicated investigators in this field has always been small, progress has been phenomenal in the century since publication of *The Origin of Species*, not only in continued discoveries of new fossils from a seemingly inexhaustible supply but also in their scientific interpretations as once-living organisms.

When Charles Darwin turned to the geological implications of his theory of evolution, his first major concern was to learn the nature of the fossil record. It is a measure of his genius that two geological chapters, ten and eleven, in *The Origin of Species* demonstrate a profound grasp of the subject far beyond that of any paleontologist of his time. It is the purpose of the present discussion to undertake briefly an evaluation of the fossil record in the light of a century of discovery since publication of *The Origin of Species*.

Darwin argued that the fossils known to science in his day represented a very small part of the potentially available record. He also understood that all of the fossils that ever existed must constitute only a very incomplete and fragmentary record of past life. These conclusions we still endorse, even though we now know immeasurably more about fossils than did Darwin. We cannot learn everything about past life from fossils, but we have learned much and the potentially knowable record is still far greater than the known record for most fossil groups. Paleontological exploration of the past is a sampling procedure in which provisional estimates of the whole are made from small, frequently biased, samples. Knowledge is cumulative and sampling errors are gradually corrected as the process is repeated over and over again by independent workers.

DARWIN'S GEOLOGICAL BACKGROUND

It is perhaps often overlooked that during his youth Darwin was by interest and training as much geologist as biologist, and it must be granted that his conclusions about organic evolution would

have been significantly different had he not learned to view organisms against the historical background provided by geology. At Cambridge University he had studied under Adam Sedgwick, who, with Murchison, was shortly to work out the British early Paleozoic sequence of rocks and fossils; but his greatest inspiration in geology undoubtedly came from Charles Lyell whose ideas were sweeping across Europe in the 1830's and bringing about a revolution in geology that had been quietly started half a century before by James Hutton.

LYELL'S CONTRIBUTION

When, in 1831, Darwin was ready to embark on the voyage of the *Beagle*, his friend, Cambridge botany professor and amateur geologist, John Henslow, gave him the first volume of Lyell's *Principles of Geology*, and the second volume, containing Lyell's views on evolution and the fossil record, was sent to him in Montevideo a year later. Henslow's gift was not only a great boon to Darwin who had not yet read Lyell's book, but it was of inestimable benefit to future science. Lyell's book freed Darwin of many of the crippling prejudices held by a majority of contemporary geologists. Lyell extended the age of the earth by millions of years and gave the rudiments of a scientific history of the earth at a time when scholars were still following Archbishop Ussher's pronouncement that the earth was created in 4004 B.C. It was Lyell who disseminated and popularized Hutton's Uniformitarian views about the adequacy of known natural laws to explain the geologic past in contradistinction to the prevailing belief, usually attributed inaccurately to Cuvier, that earth history had been characterized by successive episodes of creation and catastrophic destruction. While Lyell was not an evolutionist, his reasoned arguments against organic evolution doubtless stimulated young Darwin to consider both sides of the question and perhaps to draw parallels between Lyell's record of orderly changes in the planet and the evolutionary changes in organisms described by Lamarck.

DARWIN, THE FOSSIL COLLECTOR

It is important that Darwin thought as a geologist. His enthusiasm for the science of the earth is revealed in a letter from South America to his sisters, written in the idiom of the country gentleman (he was one of the elite and had made the Grand Tour):

> I wish any of you could enter into my feelings of excessive pleasure which Geology gives me as soon as one partly understands the nature of a country. . . . There is nothing like Geology. The pleasure of the first day's hunting cannot be compared to finding a fine group of fossil bones which tell their story of former times with almost a living tongue.

On an Argentine pampa he collected remains of extinct mammals of gigantic size and he pondered deeply on the fact that, although they clearly belonged to extinct forms, they were constructed on the same basic plan as the small living sloths and armadilloes of the region. This experience started him thinking about the fossil sequence of faunas and floras, the causes of extinction, and the origin of new forms that have replaced successively old ones in the fossil record.

DARWIN AND THE MISSING LINKS

In 1859 the fossil record still was poorly sampled and practically all paleontologic studies had been concerned with the description and stratigraphic documentation of fossil assemblages. Nevertheless, many important generalizations could be made. Although it often is denied, the known record gave strong support to Darwin and he made full use of available knowledge of fossils. The evidence that he gleaned from the fossil record showed that the prevalent theory of multiple special creations and catastrophic extinctions could not possibly explain the fossil record as a whole.

THE STRATIGRAPHIC SUCCESSION

Late in the eighteenth century Cuvier, Alexandre Brogniart, William Smith, and many others had shown the value of fossils as indicators of stratigraphic position and geologic age. Out of their observations there quickly developed the conception of a geological time scale, and the stage was set for the organization of a scientific history of the earth. In the first two decades of the nineteenth century, paleontologists were recognizing a sequence of three great time-stratigraphic units, Primary, Secondary, and Tertiary, based mainly on their fossils; and by the time Darwin returned to England from his voyage, the broad outlines of the time-stratigraphic system now in general use had been worked out in Great Britain and on the Continent (fig. 1).

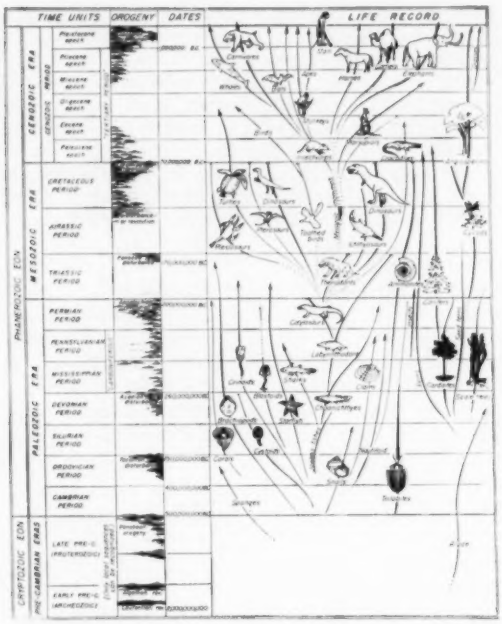

FIG. 1. The sequence of fossil floras and faunas provides the basis for a geologic time scale and worldwide correlations of events in geologic history (Dunbar, *Historical Geology*, John Wiley and Sons, 1949).

THE SUCCESSION IS GRADATIONAL

Lyell had shown that the recent biota had not appeared abruptly in its entirety, as required by special creation, but gradually, a few species at a time in the Tertiary rocks, replacing one after another species that are now extinct; and these new species and their near relatives were commonly widely distributed, making their appearance in different regions at nearly the same stratigraphic position. Darwin was deeply impressed by this and by the discoveries of de Verneuil, d'Archiac, Barrande, Adolph Brogniart, and others. They showed that there is a characteristic succession of fossil forms through time in all studied rock sequences in various parts of the world. Darwin wrote:

> Scarcely any paleontological discovery is more striking than the fact that the forms of life change almost simultaneously throughout the world. . . . Thus, as it seems to me, the parallel, and, taken in a large sense, simultaneous, succession of the same forms of life throughout the world, accords well with the principle of new species having been formed by dominant species spreading widely and varying. . . . As new and improved groups spread throughout the world, old groups disappear from the world; and the succession of forms everywhere tends to correspond both in their first appearance and final disappearance.

CONNECTING FORMS

Fossils structurally intermediate between distantly related living animals were known in Darwin's day and they, of course, influenced the strictly morphological taxonomy of the time. Many paleontologists had noted that fossil forms in some cases join together living families and even orders. For example, the fossil *Zeuglodon* was regarded as intermediate between whales and aquatic carnivores, and, after its discovery in 1861, *Archaeopteryx* was properly placed in a position intermediate between reptiles and birds, but before Darwin there was little reason to consider the phylogenetic implications of these discoveries.

CASUAL GAPS IN THE RECORD

Two kinds of interruptions in the fossil record attracted Darwin's attention and the attention of every paleontologist since. One of these is a local, or casual, deficiency which results from insufficient collecting, migrations of original organisms, unfavorable biotic environment, nondeposition, nonpreservation after burial, or destruction by erosion. With continued and geographically extended search aided by improved techniques of collecting and preparing fossils, these gaps in the record gradually are filled in as "missing links" are discovered.

Within ten years of the publication of *The Origin of Species*, Waagen had published evidence in support of an ammonite phylogeny and five years thereafter Kowalevsky had worked out a graded sequence of fossil horses in Europe. The record of horse evolution was quickly improved and amplified by Marsh's discoveries in America (fig. 2). Thus, Darwin lived to see the support from paleontology that he had confidently expected. There are now innumerable illustrations of graded temporal series of fossils from both animal and plant kingdoms, and there are few paleontologists in the world today who doubt that the fossil record gives convincing support to Darwin's thesis that species gradually become modified with time (fig. 3).

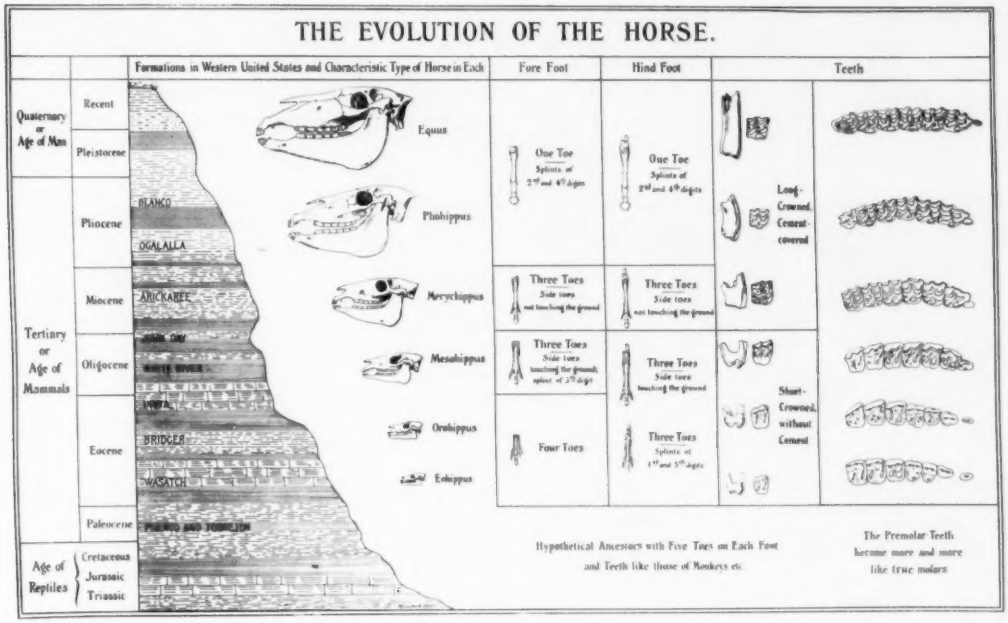

FIG. 2. The fossil record of the horse family illustrates gradual but comparatively rapid morphological change during some 60 million years (Matthew and Chubb, *Guide Leaflet Ser.* **36**, Amer. Mus Nat. Hist., 1921).

SYSTEMATIC GAPS IN THE RECORD

The second kind of paleontological break is systematic. That is, it reflects a genuine deficiency of the record not dependent on insufficient collecting or chance factors of sedimentation. The earliest members of higher categories, phyla, classes, orders, and superfamilies generally have all of the basic characteristics of those categories rather than dominantly ancestral characters. Thus, the higher categories tend to be separated sharply from other related groups with little or no tendency for intergradation. The meaning of this morphological isolation of higher categories has troubled students of the fossil record and was explained by pre-Darwinian paleontologists as indicative of special creation. It is true that a few stratigraphic levels are characterized by the "simultaneous" appearance of several higher categories, for example, at the base of the Triassic system; but for the most part the first appearances are scattered through the stratigraphic record. The idea of piecemeal special creations was not what most of the early paleontologists had in mind. A very few modern students have attributed these sudden appearances of group characteristics as evidence of large gene mutations, macroevolution, but there are alternatives that are considered more acceptable to the majority of modern evolutionists. This is the problem of the origin of higher categories.

From time to time discoveries are made of connecting links that provide clues to the relationships, as between fishes and amphibians, amphibians and reptiles, and reptiles and mammals. These isolated discoveries, of course, stimulate hope that more complete records will be found and other gaps closed. These finds are, however, rare; and experience shows that the gaps which separate the highest categories may never be bridged in the fossil record. Many of the discontinuities tend to be more and more emphasized with increased collecting.

The early history of the flowering plants, the angiosperms, is a case in point. Their rich fossil record begins with great abruptness in the lower Cretaceous rocks (fig. 4). The first angiosperm flora of some sixteen families appears almost simultaneously in such remote places as Transcaucasia, Portugal, England, Maryland, Texas, and New Zealand; and before the close of the Cretaceous

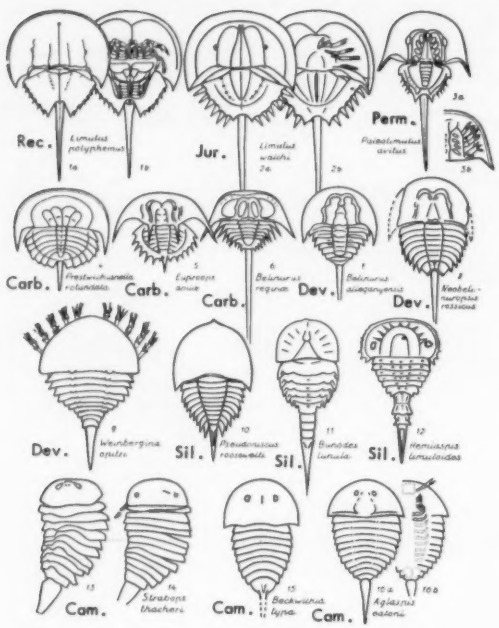

FIG. 3. The highly organized merostome arthropods have evolved very slowly during 450 million years (Størmer, 1944).

period the flowering plants had become the dominant land vegetation probably occupying most of the present niches. In spite of their initial diversity, a long and determined search for Jurassic ancestors of the angiosperms has produced only a few doubtfully related forms. We can conclude only that the character of terrestrial vegetation throughout the world underwent a radical change within a period of time that was quite brief geologically but sufficient for differentiation and worldwide spread of the angiosperms, or that a long antecedent history of these plants took place in upland habitats that have not been preserved (Axelrod, 1952).

The trilobites of Paleozoic seas also illustrate very well the phenomenon of the systematic discontinuity. Judging from their fossils, the trilobites may well have been the most highly organized, abundant, and diverse animals during the first 100 million years of their existence. Several superfamilies comprising many families appear abruptly near the base of the lower Cambrian; others are introduced somewhat higher in the lower Cambrian (fig. 5). Of the ten superfamilies of lower Cambrian trilobites, not a single ancestor is known. Several of these major groups drop out at the top of the Cambrian without known descendants. Among the post-Cambrian forms ten of the superfamilies have long and well-documented records in the later Paleozoic. But of these, seven cannot be related confidently to any of the known Cambrian groups by means of intermediate fossils. Continued collecting has only emphasized the separation of these groups in the known record.

The abrupt appearance of the trilobites near the base of the Paleozoic rocks is part of a larger problem of the origin of the Cambrian fauna. A majority of the major invertebrate phyla comprising some five hundred known species, many of which belonged to highly organized animals, are known in this fauna.

On the other hand, most pre-Cambrian rocks are unfossiliferous and very few pre-Cambrian fossils are on record. Many of these have been discredited either as inorganic in origin or younger than pre-Cambrian in age. Darwin addressed himself to this problem as follows:

> If the theory [of evolution] be true, it is indisputable that before the lowest Cambrian stratum was deposited long periods elapsed, as long as, or probably far longer than, the whole interval from the Cambrian age to the present day; and that during vast periods the world swarmed with living creatures. . . . To the question of why we do not find rich fossiliferous deposits belonging to these assumed earliest periods prior to the Cambrian system, I can give no satisfactory answer. . . . The case at present must remain inexplicable and may be truly urged as a valid argument against the views here entertained.

A century of intensive search for fossils in the pre-Cambrian rocks has thrown very little light on this problem. Early theories that those rocks were dominantly nonmarine or that once-contained fossils have been destroyed by heat and pressure have been abandoned because the pre-Cambrian rocks of many districts physically are very similar to younger rocks in all respects except that they rarely contain any records whatsoever of past life.

In Finland and the United States rare pre-Cambrian coal-like deposits have been found that may have been formed from the lowest forms of plants (Barghoorn, 1957). More convincing fossil evidence that simple plants existed nearly two billion years ago has been secured recently (fig. 17) in Ontario by Tyler and Barghoorn (1954).

Unequivocal evidence of early animal life seems to be limited to trails and burrows of soft-bodied wormlike creatures (Schindewolf, 1956). These sparse records tell us nothing about the origin of life or the course of evolution during the first three-fourths of the time that life is known to have existed on earth.

Students of trilobites, impressed by the advanced state of evolution of the earliest trilobites of the lower Cambrian, believe with Darwin that they must have had a long antecedent history in the pre-Cambrian when their skeletons may have contained little or no calcium carbonate (Whittington, 1954). It is a well-known fact that the chitinous exoskeletons of *Limulus* and other arthropods are destroyed quickly by certain bacteria and only those groups that have heavily calcified skeletons are common fossils even in Tertiary and Quaternary rocks. This explanation, however, does not take into account the fact that unequivocal fossils of soft-bodied invertebrates, although by no means common, are known in many places and should have turned up in pre-Cambrian rocks by now. The mid-Cambrian Burgess shale of British Columbia has yielded thousands of specimens of upward of 130 species of soft-bodied animals, most of which are unknown elsewhere. They are preserved with minute details as tissue-thin films of carbon imprinted on bedding planes. Many of these fossils (trilobitomorphs) are similar to trilobites but they did not possess calcareous skeletons.

A clue to the meaning of some of the systematic deficiencies of the fossil record is provided by the recent discovery of living coelacanth fishes and

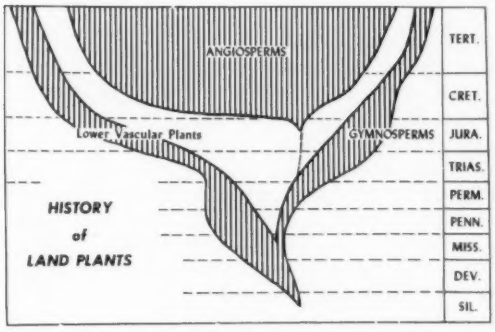

FIG. 4. The flowering plants, or angiosperms, of uncertain ancestry, appear abruptly in the fossil record and almost immediately become the dominant flora (Dorf, 1955).

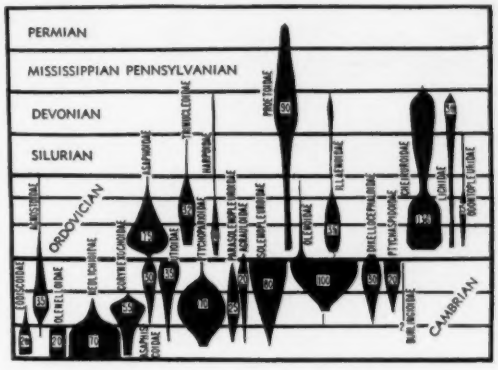

FIG. 5. Stratigraphic distribution of superfamilies of trilobites in the fossil record with numbers of known genera. Noteworthy are the contrast in composition of Cambrian and Ordovician assemblages, abrupt extinction of great groups at top of the Cambrian and restriction of post-Devonian trilobites to a single superfamily (from Moore, after Whittington, 1953).

monoplacophoran molluscs long known from the fossil record and supposed to be extinct since the Cretaceous and Devonian periods, respectively. There are many such illustrations in the fossil record of stragglers from once widespread and abundant groups that have become greatly restricted geographically, living on in some isolated area for millions of years after their disappearance in other areas. For example, blastoids died out in early Pennsylvanian times over most of the world, but they survived well into the Permian period in Indonesia, a time span of forty or fifty million years. These facts simply mean that probabilities of discovery of a fossil record or a living population are poor in those groups that are not abundant and widely distributed.

Darwin noted that our fossil record is pretty much limited to sedimentary basins. That is, low swampy areas, deltas, lakes, the sea. Organisms of upland areas and other ecological zones characterized by erosion, such as the seashore, are rarely represented in the fossil record. It has often been suggested that the angiosperms may have diverged from the gymnosperms in upland areas subject to persistent denudation. Axelrod (1958) has suggested that the late pre-Cambrian fauna may have evolved in the littoral zone of the sea, a habitat rich in ecological niches, but one which rarely is preserved in the stratigraphic record.

Simpson (1953*a*) has shown that the systematic

discontinuities in the fossil record are most satisfactorily explained as an effect of sampling error in small, isolated populations. Many of these populations were in rapid transition, undergoing "quantum evolution" between adaptive zones. Sampling is less reliable for very rapidly evolving than for slowly evolving groups. Thus, while a few connecting links are discovered between higher categories, these are relatively rare and many systematic gaps tend to persist in spite of continued collecting.

In contrast to the many fossil groups that display innumerable gaps in the record, there are a few in which the known record is relatively complete and inferred phylogenies are secure, e.g., the ammonites (fig. 6).

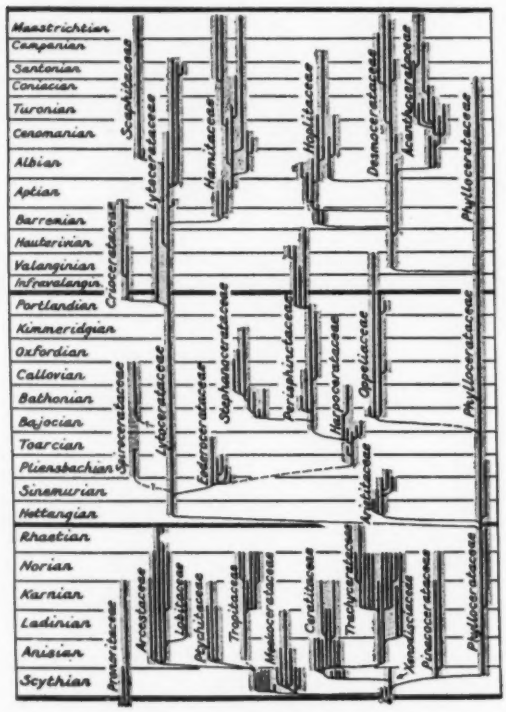

FIG. 6. Stratigraphic distribution and inferred phylogeny of Mesozoic ammonites. Heavy horizontal bars separate Triassic, Jurassic, and Cretaceous systems and shaded areas represent superfamilies and family subdivisions. The Triassic ammonites originated from two, and the Jurassic forms from a single superfamily (from Moore, 1955).

ABUNDANCE OF FOSSILS

One of the earliest discoveries about the paleontologic record is that fossils actually are more abundant in fossil-bearing rocks than might be assumed from cursory inspection. In many cases it may be suspected that even those forms represented in collections by a few specimens, or only one, are numerous or abundant within the rocks.

Now, the problem of locating fossils is enormously complicated by the fact that fossiliferous strata are partly or wholly concealed in most areas by a cover of superficial rubble, soil, and vegetation. Consequently, our ideas about the abundance of fossils usually are colored by the character and extent of suitable rock exposures.

Strata considered to be only sparsely fossiliferous as judged from superficial inspection actually may be abundantly so. The degree to which this is true is clearly shown by methods of mass collecting fossils, wherein a volume of fossiliferous clay or marl is dug by hand shovel, or power machinery, washed with water, and sieved for fossils. This method has long been used widely for microscopic fossils such as spores and Foraminifera, but it also is coming into use for larger invertebrates and bones and teeth of small vertebrates. The number of fossils thus obtained is usually greater per unit volume of rock than per unit surface and fossils collected in matrix have an advantage that they are damaged less frequently by weathering than those found at the surface.

Small fossils are incredibly numerous in certain strata, where they may be a major component of the rocks. Leidy once estimated a quarter of a million Foraminifera in an ounce of marine sediment. A cubic inch of diatomaceous earth contains as high as fifteen million diatoms per cubic inch and there are many cubic miles of pure diatomite in the Tertiary rocks of California alone. Robert Broom, the distinguished South African paleontologist estimated that there are about eight hundred billion skeletons of vertebrate animals in the Karroo formation. While such estimates are not really meaningful in themselves, they stress the vast difference between the paleontological sample and the astronomic numbers of fossils remaining in the rocks. The abundance of individual fossils is, of course, not directly related to their diversity. Teichert (1956) has undertaken an interesting estimate of the total number of fossil species of animals and plants. He has taken as a premise

that those organisms with skeletal parts make up most of the fossil record and he omits consideration of soft-bodied organisms or insects as quantitatively unimportant. In this he errs on the side of conservatism because very many of these are known as fossils. Among living organisms the numbers of species most susceptible to preservation as fossils are:

Invertebrates	170,000
Vertebrates	49,000
Vascular plants	350,000
"Preservable species"	569,000

Taking twelve million years as the average longevity of a species, he concludes that the number of species of animals and plants preserved in the rocks may reach a total of ten million. According to an estimate made by Muller and Campbell (1954), about ninety-two thousand fossil species of animals are now described (fig. 7),

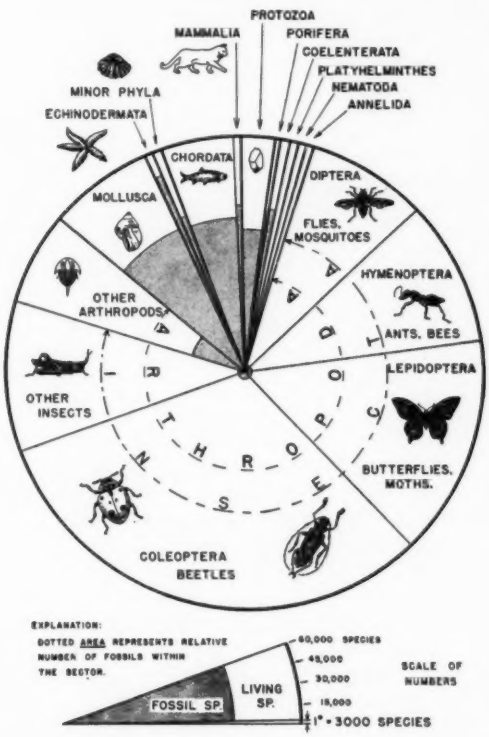

FIG. 7. Relative numbers of known species of animals (Muller and Campbell, *Systematic Zool.*, 1954).

and I think that the plants would bring the total to around one hundred thousand or only one per cent of Teichert's estimate of the ultimate richness of the fossil record. These speculations are useful in stressing the fact that the fossil record still is poorly known, and they indicate something of the magnitude of the opportunities and the task ahead.

Publication rates provide a rough measure of the rates of discovery of new categories of fossils (fig. 8). A long sustained or increasing rate of publication of new genera, for example, is strong circumstantial evidence that there has not been a decline in the rate of new discoveries. Minor fluctuations in publication rates are produced by the sporadic appearance of monographs, by differences in initiative and taxonomic philosophy among authors; and larger fluctuations are caused by war, depression, and other vicissitudes of life. Long term trends may be significant in terms of the development of knowledge about fossil groups. Figure 8 indicates that discovery rates in Foraminifera and fossil mammals seem to be expanding. There is no indication from this evidence that most of the distinctive kinds of fossils have been discovered. On the other hand, discovery of new living mammals has about ceased, and there is a suggestion that the rate of discovery of new ammonoids is declining. This may indicate that most of the basically different kinds of ammonoids have been found, but it is too early to be sure of this.

BIAS IN THE FOSSIL RECORD

It is an exciting experience, charged with emotion, to sit in a canoe quietly drifting down a stream surrounded by a tropical forest teeming with life or to submerge oneself along a coral reef and to inspect closely this biota. To the paleontologist these are momentary situations in a changing scene—single frames in the motion picture of earth history. How much is likely to be preserved in the fossil record? I have examined the alluvial deposits of the tropical river bank for recently deposited organic remains and I have studied broken fragments of living coral reefs piled above sea level by great storm waves. In both cases, the contrast between the living and the dead is very great. Practically all of the organic substances readily decomposable by aerobic bacteria and fungi disappear within days or weeks. In the river alluvium there are remains of perhaps ten or fifteen species of the total of ten thousand. In the reef limestone fifty to

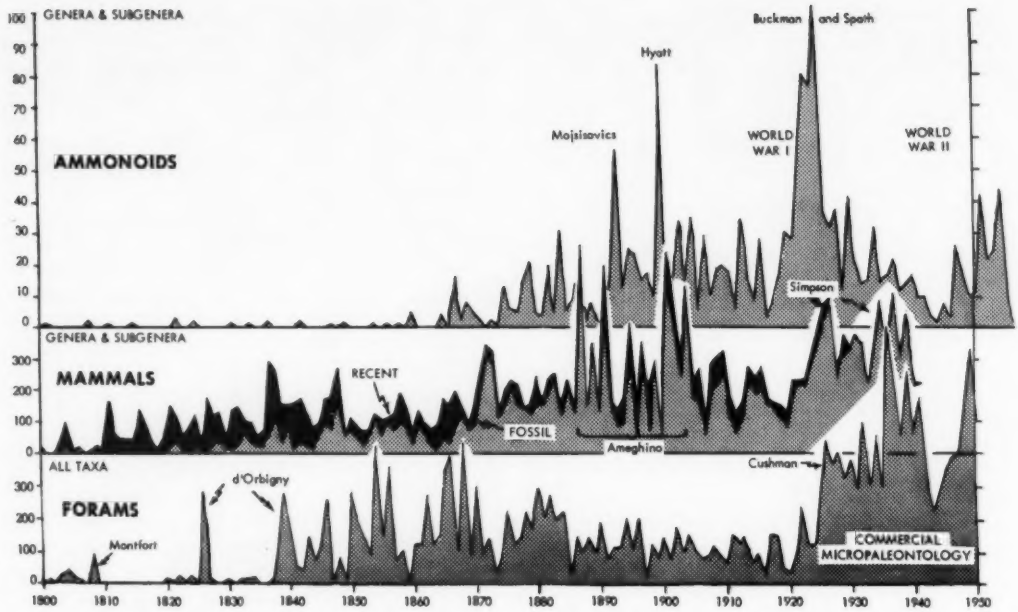

FIG. 8. Publication rate as a measure of discovery rate of new fossils. Minor fluctuations result from initiative of a few authors, larger cycles reflect economic and political conditions. The data suggest that most living mammals are now known but fossil mammals and Foraminifera are being discovered at increasing rates. New ammonite discoveries possibly are decreasing in frequency. (Ammonite data from Arkell, Wright, and Kummel, *Treatise on Invertebrate Paleontology*, 1957; mammals from Simpson, 1945; Foraminifera from Messina, 1952.)

seventy-five species of the living three thousand are recognizable after depredations of bacteria and scavengers. But note this: even though the living communities are not preservable in the aggregate, the few preserved species, studied in context with the sediments, tell eloquently of a specific habitat.

Darwin showed clearly that the fossil record probably is never a random sample of life of the past. This idea extends back to Cuvier and beyond.

A RECORD OF SKELETONS

Aside from extremely rare examples of preservation of animal tissues in comparatively young rocks and small arthropods and spores in fossil amber, nearly all fossil remains consist of comparatively resistant hard parts. Complete skeletons with all of the parts in position of articulation are on the whole exceptional or even unknown for many groups of plants and animals, so that paleontological studies usually are based on scattered and fragmentary parts of skeletons. Although there are exceptions, the organs and other tissues, details of form, coloration, behavior, and many other characteristics of living organisms commonly are not preserved. The great hosts of soft-bodied plants and animals that make up a large part of any biota likewise rarely are preserved so that their very existence in the past must be inferred by analogy with communities of organisms of the present.

UNEQUAL PRESERVATION OF HABITATS

There are puzzling systematic deficiencies in the records of many groups of organisms with skeletal parts well adapted for fossilization. The incompleteness of the record in many cases probably originates in low population density, location of habitat far from sites of deposition of sediments, and in the habits of organisms. For example, as already noted, the fossil record throughout the world is very poor in remains of upland animals and plants. Probabilities of quick and permanent burial of these forms are slight because they live at a distance from the low places where sediments finally come to rest in depositional basins. Like-

wise, arboreal mammals and birds tend to be consumed by scavengers before burial and they are poorly represented as fossils. There is scarcely any record of desert plants. Desert deposits are deficient in fossils of all kinds because of a characteristic sparseness of desert life, and oxidizing conditions and leaching reach far below the surface. Organic remains are destroyed here about as fast as they are buried; desert deposits tend to be coarse-grained. The sediment fragments grind up organic remains as they are transported in violent floods that characterize stream deposition in the desert.

Without going into all the various factors operative in these systematic deficiencies in the fossil record, it seems safe to conclude that very many organisms did not frequent sites of persistent and quiet accumulation of sediments. For one reason or another they did not occur in abundance in places where they might be buried quickly. The extreme rareness of fossil remains of early man is a case in point. Man and many other mammals make use of their intelligence in escaping flood waters and in avoiding quicksands and bogs.

On the other hand, aquatic organisms and those that live near water are in close association with the deposition of sediments and are favorably situated for quick burial before they are consumed. Consequently, the greatest part of the fossil record consists of the skeletal remains and traces of organisms that lived in water, especially in the sea, or near the margins of streams, lakes, or swamps. Thus, in a very real sense, most of the fossil record is the record of lowland or marine basins of aqueous sedimentation. Even under the most favorable conditions, however, quick burial and preservation of organic remains must be a rare event as compared with the total number of organisms that live at one time.

BIOLOGICAL FACTORS

Population density and distribution must also be an important factor affecting the frequency with which organisms have been preserved. It seems certain that preservation of organisms in the fossil record is such a very rare event that thousands or millions of individuals are destroyed for each one that is incorporated in the record. Thus, organisms that are abundantly represented in an environment favorable for quick burial have a better chance of preservation than those that are not so abundant. In general, small organisms reproduce more rapidly and produce larger populations than do large organisms. It is perhaps partly because of this that fossil Foraminifera are more abundant in the rocks than, say, mammals. Probably the relative sparseness of larger fossils as compared with microscopic forms is a reflection of differences in relative abundance.

The structure of the plant body is not well adapted to preservation as a single unit and the most common plant fossils are detached spores, pollen leaves, stems, or fragments of wood. Well-preserved seeds, fruits, and particularly flowers are rare. There also is occasionally a close resemblance of form among the leaves of different families and orders. These difficulties are overcome by careful consideration of all the fine details of shape, texture, character of margin, and apex of leaves, character of primary and secondary venation, and particularly by the microscopic structure of the cuticle of leaves and reproductive organs. Epidermal characters are often well preserved and directly comparable to those of living plants. Thus, conclusions are not based solely on a few leaves but on a whole complex of characters and on the plant associations which, although incomplete, are nevertheless composed of dominant members of harmonious communities and therefore indicative of specific habitats.

PHYSICAL FACTORS

Fossils may be destroyed quickly by weathering or gradually by changes that take place after burial. These changes are more rapid in certain kinds of skeletons than in others so that there is selective preservation of some fossil groups over others.

The processes of sedimentation in many cases complicate interpretation of the associations of fossils, particularly the small forms that are easily moved by wind or water. The dead remains of various forms may be transported from diverse habitats and deposited together in associations that do not reflect any single life environment. Under these conditions there is much winnowing and sorting of organic remains by size, shape, and effective specific gravity. The remains of young and small organisms thus may be separated from those of older and larger forms. Less commonly, the fossils of an older rock formation are weathered free of rock matrix and become incorporated in a younger formation in association with fossil forms that lived much later and under quite different conditions.

These are all complicating factors that try to the utmost the skill and patience of the paleontologist. Nevertheless, they do not provide insurmountable obstacles to correct interpretations of the record. As in all scientific research, paleontological interpretations may be from time to time independently tested by additional work and new discoveries.

In spite of the shortcomings of the fossil record, many extinct animal and plant groups favored by the factors of preservation are becoming quite well known. The record provides documents of organic evolution and still incomplete but very meaningful histories of many important groups of organisms through hundreds of millions of years. It serves as the basis for a scale of geologic time that has been adopted generally and found accurate in broad outline throughout the world. The sequence of fossil faunas and floras enables the paleontologist to date rock formations in terms of this standard geologic scale and thus to correlate contemporaneous strata and geological events in widely separated regions.

RELIABILITY OF THE RECORD

I have discussed at some length the shortcomings of the fossil record as a representative sample of past life. Darwin understood very well most of the cited limitations. He was optimistic about the future of paleontology, and the remarkable advances in the past century of discovery and collecting surely have far exceeded his expectations. But how can we evaluate our knowledge of the record? What are the confidence limits of our present inferences? How much will we have to modify our conclusions as more information is gathered? These questions cannot be answered readily, but past experience may help us in formulating tentative judgments.

THE TEST OF ADEQUACY

Experience from past discoveries shows that our ideas still are changing rapidly in some areas of knowledge as new evidence accumulates. In other areas, there has been little or no fundamental change in broad perspective for several decades in spite of continuous study. For example, the early nineteenth century paleontologists knew that the trilobites were quite varied and complex at their first appearance in the lower Cambrian, that they soon deployed greatly in the higher Cambrian and Ordovician rocks, and that they then gradually diminished in variety until their disappearance from the record near the top of the Paleozoic.

Even if the known range of the trilobites is extended through future discoveries of pre-Cambrian or Triassic trilobites, it would be unreasonable in the present advanced state of knowledge to consider seriously the possibility that the new finds would reveal widespread and diverse faunas at the new limits of range that had been completely overlooked previously. Such new discoveries are not likely to affect greatly our present conclusions about the presently known record.

Studies of fossils over the past century have confirmed many generalizations held in Darwin's day, and, in retrospect, we can recognize steady confirmations as well as refutations of general conclusions. We still believe that the dinosaurs, marine reptiles, and the ammonites dropped out in the late Cretaceous. Gymnosperms are still considered dominant in Jurassic and Triassic rocks; angiosperms and mammals are dominant in Tertiary rocks. Of course, revolutionary discoveries occur from time to time, but usually they result in modification and adjustment of details, not in wholesale abandonment of broad generalizations arrived at empirically after much sampling. The known record is spotty indeed, but it is very good for the more abundant and well-preserved groups of fossils. When fossils are rare or poorly preserved, conclusions are more tentative and they vary greatly in order of probability.

EVOLUTIONARY PATTERNS

The great times of expansion and recession of the better-known major groups have been known for a long time and the general outlines of knowledge here are not likely to undergo major revision. Some major groups display what appears to have been a sort of ecological incompatibility, successively and gradually replacing one another in time as more successful groups wrested one niche after another from competing inferior groups. Darwin anticipated this phenomenon and suggested how competition could lead to the extinction of all of the less well-adapted organisms without concurrent changes in the inorganic factors of the environment. Illustrations of replacement in competing groups are the trilobites, shelled cephalopods, and bony fishes; the creodonts and fissipeds; and the perissodactyls and ruminant artiodactyls (fig. 9). Among plants, the expansion of the angiosperms was accompanied by

restriction and elimination of many groups of gymnosperms and lower land plants (fig. 4).

RATES OF EVOLUTION

Studies by G. G. Simpson and others have shown that the known fossil record now is sufficient for accurate measurement of rates of evolution, a subject of great importance in connection with understanding evolutionary mechanisms and also of interest from the standpoint of geological chronology (Simpson, 1953*a*). It now is well established that rates of evolution vary greatly within and between related groups. Furthermore, there is no simple correlation between reproduction rate and evolutionary rate. Certain groups of small Foraminifera, with reproductive rates thousands of the times those of mammals, have evolved very much more slowly than the latter, but other Foraminifera have evolved as fast as any group of mammals. High, intermediate, and low rates are recognized and these are dependent on the Darwinian factors of variability and selection pressure (figs. 2, 3, 6).

PHYLOGENY

Phylogenies in paleontology are inferred from morphological series distributed chronologically through the stratigraphic succession. Innumerable examples have been worked out for Foraminifera, corals, molluscs (fig. 6), echinoderms, arthropods, hemichordates, vertebrates, and vascular plants. The evidence in many fossil groups is so well documented and voluminous that few neontologists would think of ignoring paleontologic data in making phylogenetic interpretations. For example, Florin (1944) has shown that the mutual relationships among modern conifers can be understood only by taking into account the many extinct Permian forms which had fructifications unlike those of any living forms. It has been shown many times that modern animals and plants are the ends of evolutionary lines which usually are more specialized in at least a few characters than the most closely related ancestral forms in the fossil record. Thus, hypothetical phylogenies based solely on living genera and species cannot express the true relationships. In order to understand the ancestry of, and connections between, living genera and families, it is necessary to know the fossil record. Conversely, the evidence from fossils is incomplete without reference to distributions, ecology, anatomy, and adaptations of living forms.

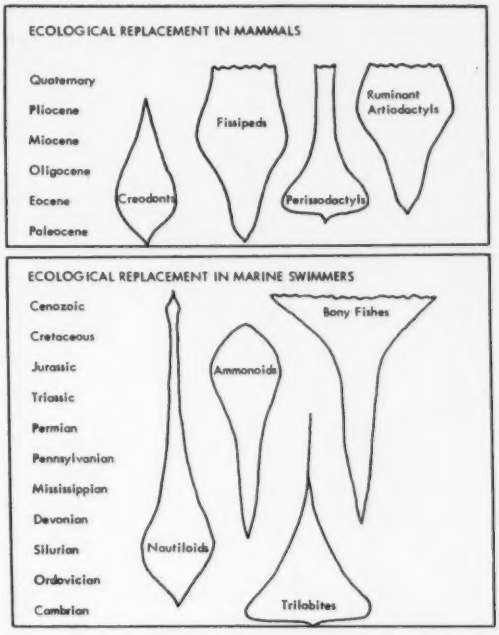

FIG. 9. Replacement among competing major groups of animals. The patterns of increasing and decreasing diversity suggest progressive ecological displacement of less successful by more successful groups. (Data on mammals after Simpson, 1953, Columbia Univ. Press.)

Paleontologists have pioneered studies of growth and morphogenesis and they have provided many illustrations from the fossil record of correlated growth (allometric) gradients in both ontogeny and phylogeny (fig. 10).

One outstanding contribution of paleontology that would otherwise be completely unknown is the repeated demonstration of long evolutionary trends in which two or more separate but related lineages pass independently through the same sequence of morphological changes, either simultaneously or at different times (fig. 11). Many illustrations are known among both animals and plants. For example, there was a persistent tendency for many lines of primitive graptolites to change direction of colony growth from downward or horizontal to vertical. This trend extended through several families and it frequently enables the stratigrapher to determine the general geological age of a graptolite assemblage from evolutionary stage without identification of the

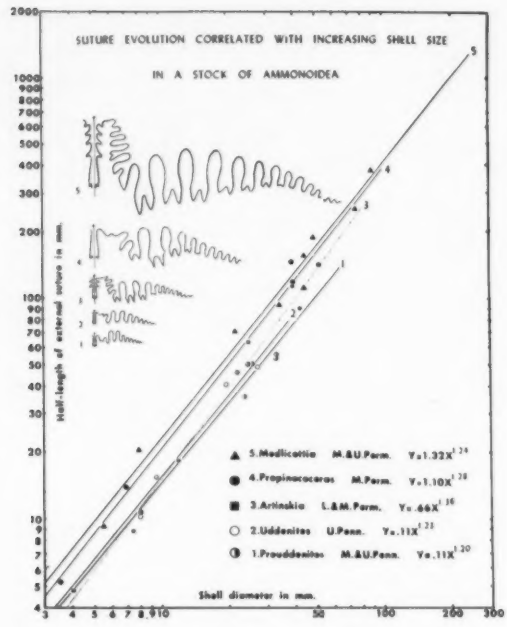
SUTURE EVOLUTION CORRELATED WITH INCREASING SHELL SIZE
IN A STOCK OF AMMONOIDEA
Half-length of external suture in mm.
Shell diameter in mm.
5.Medlicottia M.&U.Perm. Y=1.32X^1.29
4.Propinacoceras M.Perm. Y=1.10X^1.28
3.Artinskia L.&M.Perm. Y=.66X^1.16
2.Uddenites U.Penn. Y=.11X^1.33
1.Prouddenites M.&U.Penn. Y=.11X^1.20

FIG. 10. Correlated trends in evolution of certain ammonites. There is a simple mathematical (allometric) relationship between the tendency for shells to increase in size and increased complexity of suture pattern during evolution. A close relationship is found between size and complexity during growth of the individual (Newell, *Evolution*, 1949).

particular genera at hand (Bulman, 1955). Likewise, many families of the great groups of corals have evolved along a characteristic sequence from solitary or dendritic forms to tightly packed colonies with prismatic individuals (Wells, 1956). The independent development of saber-toothed "tigers" and carnivores in placental and marsupial mammals, the closely parallel changes in horse and horselike litopterns, the common trends for increased body size and brain size in mammals are other examples of parallel evolution recognizable as such only in the fossil record (Colbert, 1955).

Stebbins notes that "the great majority of evolutionary trends toward increased specialization in vascular plants can be explained as a result of three types of morphological trends, acting either separately or in conjunction with each other. These are reduction, fusion, and change in symmetry. The most widespread of these trends has been reduction" (Stebbins, 1950).

These parallel trends no longer have orthogenetic or vitalistic implications to the majority of paleontologists who now recognize the probability that these patterns are an adaptive expression of similar genetic organization in closely related lineages.

FOSSIL POPULATIONS

The fossil record supplies a wealth of data on changes in time and space in both populations and entire biotas during long spans of time. Thus, paleontology contributes evidence bearing on many principles of evolution and gives the paleontologist an advantage of an abundance of time that is denied the student of living organisms.

Many fossil samples are adequate for quantitative studies of various kinds. For example, Kurten (1953), Deevey (1955), and others have shown that relatively undisturbed fossil assemblages may be used effectively in studies of population dynamics. Samples suitable for the studies of population variability are quite easily obtained for some groups, especially microfossils; and

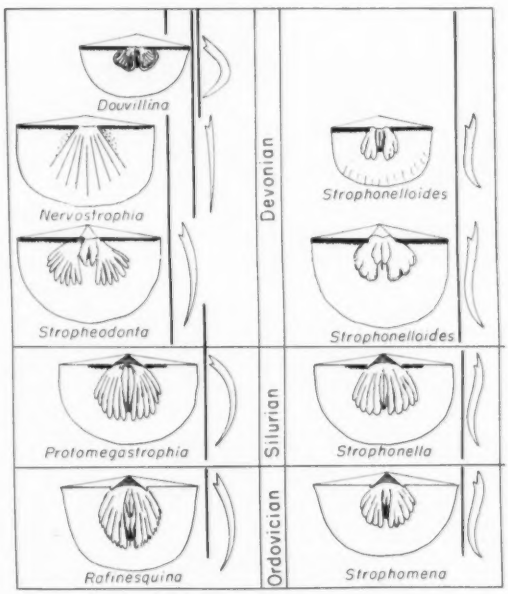

FIG. 11. Parallel evolution in two families of early Paleozoic brachiopods. In both lines the hinge margin becomes increasingly subdivided by interlocking teeth. Note that the rates of change were about the same in the two stocks (Dunbar and Rodgers, *Principles of Stratigraphy*, John Wiley and Sons, 1957).

statistical methods (fig. 12) are used increasingly to refine discrimination and to establish the limits of fossil subspecies and species (Imbrie, 1957).

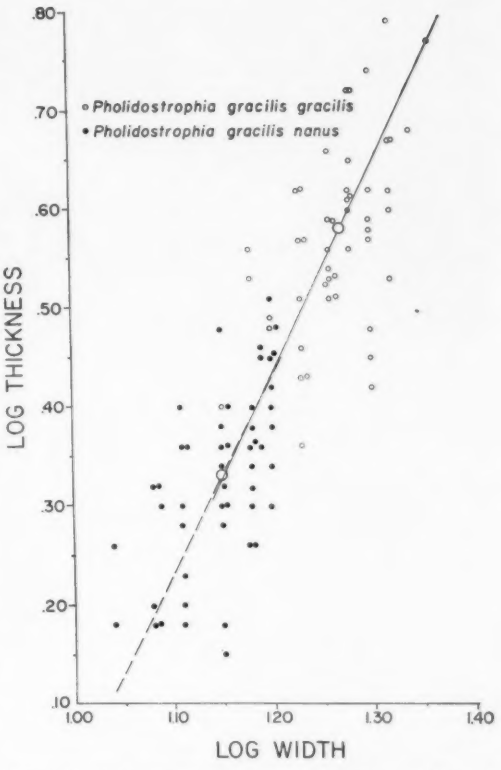

FIG. 12. Evolving variable fossil populations of brachiopods in some cases may be distinguished only by statistical comparisons. The two populations treated here are considered to represent chronological subspecies (Imbrie, 1956).

PALEOECOLOGY

Much attention has been given in recent years to ecological interpretations of fossil assemblages in order to learn about the mutual relationships between past organisms and their environments. This requires a disciplined synthesis of paleontology, stratigraphy, petrology, geochemistry, and sedimentation for the most complete utilization of all available evidence from fossils, rocks, and stratigraphy. By attacking paleoecological problems along all available lines of evidence, surprisingly detailed interpretations of past environments are possible and the fossils themselves acquire much added significance whenever they are studied in the full context of their geologic setting (e.g., Imbrie, 1955; Newell *et al.*, 1953; Bradley, 1931).

Fossils have provided most of the evidence for a quite detailed history of changes in distributions of land and sea, and many generalized paleogeographic maps have been published showing the location of major seaways and lands for the successive epochs of time (Dunbar, 1949). These maps are helpful in summarizing knowledge of the distributions of marine and nonmarine deposits and in working out hypothetical times and routes of migrations of organisms (Simpson, 1953*b*).

The evidence from fossil plants is in some respects less complete than that available from fossil animals, but plants tell us much more than animals do about past climates and there is an excellent record of the succession and migration of floras during geologic history.

The oldest known fossils are the remains of filamentous algae and fungi (fig. 17), but the record of past floras is quite poor before the upper Silurian by which time the continents of the world had become clothed with a diverse vegetation of vascular plants (fig. 4). Cosmopolitan floras of extraordinarily wide distribution of the middle Paleozoic are thought to indicate much milder world climates than at present with remarkably little zonation. The late Paleozoic and Triassic floras increasingly marked zonation roughly parallel with the present equator. This is succeeded in Jurassic and Cretaceous rocks by comparatively uniform floras throughout the world. Evidence of latitudinal floral zones is again apparent throughout the Tertiary period which was a time of gradual cooling from generally subtropical conditions at intermediate latitudes to the present conditions (fig. 13). The zonal distribution from fossil floras argues for stability of the poles and continents throughout the latter part of earth history (Chaney, 1940; Edwards, 1955), as opposed to extensive polar migrations or continental sliding as suggested by studies of paleomagnetism. The record of fossil invertebrates has been used in arguments for (Ma, 1957) and against (Stehli, 1957) migration of poles or continents. All paleontologists are agreed that the record indicates mild and surprisingly uniform climatic conditions throughout much of geologic time in contrast to the sharply zoned climatic conditions of the past million years.

Fossil spores long have been known in coal beds

FIG. 13. Evidence from fossil plants of progressive cooling of climate since the Cretaceous period. The glacial climates of the Pleistocene are not represented (Dorf, 1957).

(fig. 14A), and in the past few decades plant micropaleontology, or palynology, as it is now termed, has produced a vast literature of thousands of papers on fossil spores and pollen, bearing particularly on stratigraphic zonation and correlation in coal basins and Quaternary nonmarine deposits. These fossils have assumed a significance for correlating and dating continental deposits comparable to that of the Foraminifera of marine rocks. The tiny plant fossils are chemically resistant and may be extracted successfully from rocks by chemical means. In 1900 the Swedish botanist Logerheim showed that the stratigraphic succession of spores and pollen in Quaternary deposits provided a detailed record of floral migrations under the influence of strong climatic changes. With the aid of these tiny plant remains, the complex climatic fluctuations of the Quaternary glacial and interglacial stages have been worked out in great detail.

Shortly after World War II, H. C. Urey showed that the ratio of the isotopes of oxygen O^{18}/O^{16} contained in unmodified calcium carbonate skeletons of aquatic organisms is a delicate indication of the temperature of the water in which the skeletons were secreted. Paleotemperatures of ancient marine molluscs as old as Cretaceous thus have been measured, but the greatest application of this chemical method has been to work out the detailed stratigraphy and temperature zonation of the Globigerina ooze that blankets much of the floor of the north Atlantic (Emiliani, 1958*a*). The records of climatic fluctuations over the north Atlantic basin throughout the glacial

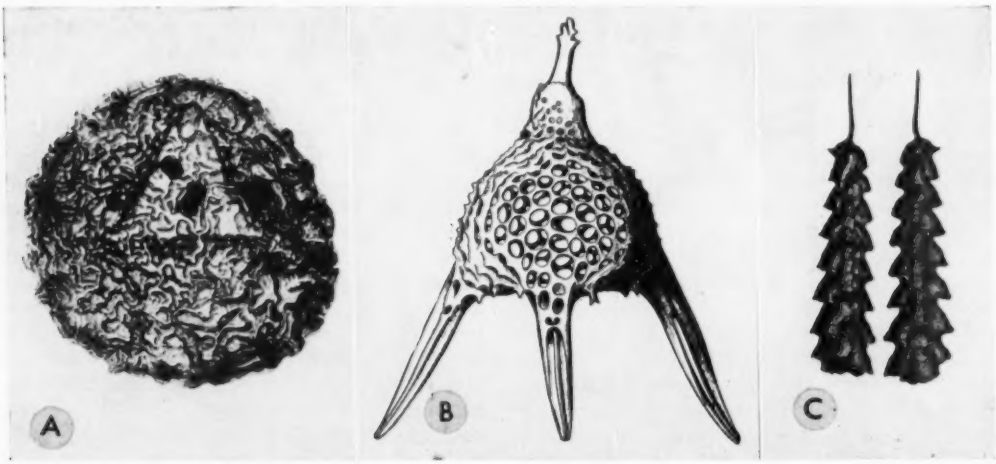

FIG. 14. Microscopic fossils. A, a plant spore, × 250, of Mississippian age, Nova Scotia (Hacquebard, 1957, *Micropaleontology*); B, a silica radiolarian, × 250, late Tertiary, Rotti (Riedel, *Jour. Paleont.*, 1953); C, an uncrushed graptolite colony of original chitinoid material, × 8, Ordovician of Öland (Bulman, *Archiv för Zoologi.*, 1936).

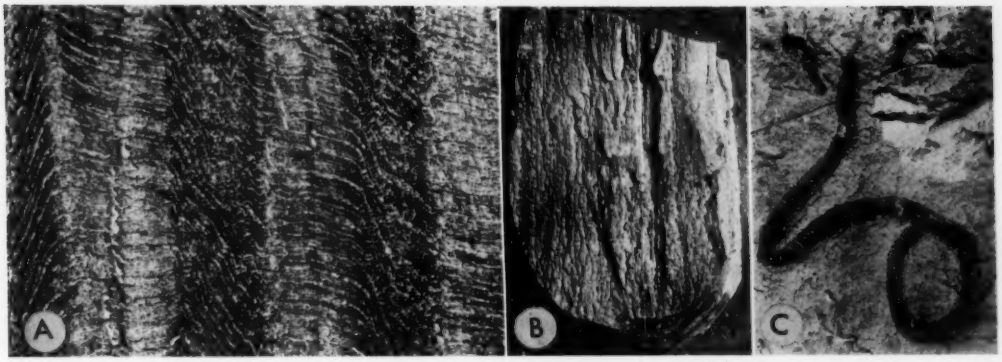

FIG. 15. A, B, fossil wood of Araucaria tree more than 100 million years old. The microscopic structure of this early Cretaceous fossil from New Jersey is perfectly preserved. The wood has not been mineralized or otherwise appreciably modified. A, × 16; B, × 1; C, fossil annelid worm with details preserved as carbonaceous film on clay-shale, × 3, upper Cambrian (Tremadocian) of England (Whittard, *Quart. Jour. Geol. Soc. London*, 1953).

and interglacial stages of the past 300,000 years have been worked out in detail and correlated with climatic cycles in Europe and America determined by means of pollen analyses (Emiliani, 1958*b*).

QUALITY OF FOSSILS

Much has been written and said about the imperfections of fossils which, for the most part, consist of incomplete, weathered, or fragmentary skeletons, or their impressions in matrix from which the skeletal remains have been dissolved by ground water. Fortunately, we do not have to depend solely on fossils of inferior quality for our information about past life. Steady improvement in techniques of collecting and of extracting fossils from rock matrix has effected a minor revolution in paleontology and has shown that there is a bountiful supply of well-preserved material available for study provided that it can be suitably prepared for study. The great impediment to progress in paleontology is not the imperfections of the fossil record, but rather the difficulties involved in freeing fossils from matrix or otherwise preparing them for study. A large part of the energies and time of paleontologists is spent in freeing fossils from matrix in the laboratory.

Animal skeletons and shells originally composed of phosphate or carbonate of lime, or of silica, and leaves, spores and the woody parts of plants form the bulk of the fossil record and these may be well preserved (figs. 14B, 15), but there are also examples of preservation of chitinous skeletons and soft tissues which provide valuable information not available in the more common fossils (fig. 15C).

PRESERVATION OF SOFT PARTS OF ORGANISMS

For example, frozen mammoths with parts of the flesh and skin preserved have been reported from more than fifty localities in northern Siberia, and thousands of ivory tusks have been obtained from this source and marketed for the manufacture of art objects in China. In this case, continuous refrigeration since death has prevented bacterial decay. Fossils preserved in this way are limited to quite young fossils of the far north. A much more important mode of preservation is the embalming action of stagnant, oxygen-deficient waters of certain swamps, lakes, and marine basins. Anaerobic conditions prevail where products of decaying organic matter become so concentrated that they suppress the activities of decay bacteria.

Animal tissues decompose very slowly in the bottom sediments of stagnant waters. For example, a large number of human cadavers more than two thousand years old have been found within peat deposits of Denmark and Holland (fig. 16A). Many of these are remarkable for the excellent preservation of tissues and organs which have suffered hardly any shrinkage or deformation. Experimental work by Franz Hecht indicates in a general way how animal tissues may be preserved for a long time after burial. The observations were made at the Senckenberg-am-Meer Institute near Wilhelmshaven (Hecht, 1933). Fish carcasses were buried in

FIG. 16. A, Tollund man, one of many bodies preserved for 2,000 years with but little deterioration in recent peat bogs of Denmark (P. V. Glob, *London Illust. News*, 1951); B, fossil bacteria on surface of trachea of beetle, × 800, Eocene lignite deposits of Geisel Valley, Germany. These have not been mineralized (Mrugowsky, *Nova Acta Leopoldina*, 1936).

the fine-grained sediments of tidal flats or in aquaria and studied at intervals. The body of a shark, naturally stranded on tidal flats in 1924, was buried beneath three feet of sediment. It was unearthed in 1926 and again in 1931, and studied. Surprisingly, it had changed very little in form. From his studies Hecht concluded that the albuminous substances decomposed rapidly (presumably liberating ammonia in the process), but the fatty substances decomposed very slowly and gradually passed into the enclosing sediment sealing the organic mass concretion-like from ground waters and oxygen. Under certain conditions the environment was acid and the skeletons of associated clam shells were dissolved. Extreme anaerobic conditions prevailed when sulfate-reducing bacteria were active. In this case the interstitial water became alkaline because of replacement of the strongly acid sulfate radicle by sulfide, and calcareous skeletons were perfectly preserved. Hecht's work is so suggestive that further experiments along these lines should be undertaken.

Incompletely decayed plant remains accumulate in bogs as peat, and if the peat becomes buried by sediments, it may eventually form coal through a succession of chemical changes. Remains of bottom animals are not abundant in these deposits because bog waters are usually anaerobic and even toxic, but occasional insects and land animals find their way into bog deposits where, free from the depredations of scavengers, they may become preserved as fossils.

One of the most remarkable examples of preservation of organic tissues in antiseptic swamp waters is a "fossil graveyard" in Eocene lignite deposits of the Geisel Valley in central Germany. This was systematically studied by Johannes Weigelt of Halle University and his associates (Weigelt, 1935). Many animals, including groups rarely found as fossils, lower primates, snakes, and birds were trapped in several small, scattered bogs where they accumulated and were preserved from bacterial attack in stagnant oxygen-poor waters. More than six thousand remains of vertebrate animals and great numbers of insects, molluscs, and plants were found over a period of several years as the lignite was being mined.

The fossils that had been collected when Weigelt made his report in 1935 included more than fifteen hundred fish of many kinds, twenty frogs, a salamander, fifty-two crocodiles, two hundred tortoises, several snakes, and tree lizards, twenty different kinds of birds, seventeen species of lemuroids, five rodents, six archaic carnivores, three early horses, a bat, and many primitive herbivores.

The flattened and dessicated remains of soft tissues of these animals in many cases showed details of cellular structure. Some of the specimens had undergone little chemical modification, but among the frogs there are specimens in which the bones were leached away while the brain and spinal cord were preserved as *adipocere*, a calcium compound of fatty acids. This is a very unusual case of preservation of soft anatomical structures after destruction of the hard skeleton. Epithelial cells showing the nuclei were preserved in the skin of frog specimens. Small details of fly larvae and beetles, including the chitinous exoskeleton, muscular tissue, and tracheae were preserved. Muscular tissue, connective tissue showing microscopic details, and cartilage were found in fishes, frogs, salamanders, lizards, and mammals.

Several fossils contained remains of fat cells and pigment cells (chromatophores) with animal pigment. Well-preserved bits of hair, feathers, and scales probably are among the oldest known examples of essentially unmodified preservation of these structures. Stomach contents of beetles, amphibia, fishes, birds, and mammals provided direct evidence about eating habits. Bacteria of two kinds were found in the excrement of croco-

diles and another on the trachea of a beetle (fig. 16B). Fungi were identified on leaves, and the original plant pigments, chlorophyll and coproporphyrin, were found preserved in some of the leaves. From such ample fossil evidence it is possible to reconstruct the Eocene life of the Geisel Valley in considerable detail.

Fossil wood buried under the anaerobic conditions of stagnant swamps has in some cases endured with only little decay for amazingly long periods of time. For example, logs found in the Eocene lignites of Germany and in early Cretaceous clays of New Jersey are composed of unaltered wood and show perfectly preserved microscopic cellular structure of the original trees (figs. 15A, B). They resemble ordinary wood and do not exhibit significant mineralization in spite of the fact that they are approximately fifty million years old in the first case, and one hundred million years old in the second.

The fossil amber deposits of the Baltic region are famous for the well-preserved insects and spiders found in the amber. These were trapped in tree gum long ago, in the Oligocene epoch, and have been protected from decomposition by the moisture-proof and air-proof cover.

Destruction of organic remains is retarded in impervious rocks which not only exclude oxygen but also prevent the circulation of ground water. Molluscs of Cretaceous age are abundant in the Coon Creek Clay of Tennessee. The mother-of-pearl shells and even chitinoid ligaments of clam shells are extraordinarily well preserved for faunas this old. Caster and Waering (1951) discovered many remarkable skeletons of eurypterid *Megalograptus* in a clay deposit of Ordovician age. The original chitin is but little altered in these fossils and still retains a scorpionid color pattern, and many of the skeletons are articulated. Since chitin usually is quickly destroyed by bacterial decomposition, the preservation of these eurypterids illustrates the influence of the type of matrix on preservation of fossils. The horny substance of graptolites still is preserved in calcareous rocks of fine grain (fig. 14C).

FOSSILS IMPREGNATED WITH SILICA

The most effective preservative of fossils is fine-grained silica which may hermetically seal and protect organic remains from bacteria and ground water solutions for hundreds of millions of years. The most remarkable examples of this are filaments and spores of low algae and fungi found in the chert of the mid-Huronian Gunflint formation of Ontario. The oldest known fossils,

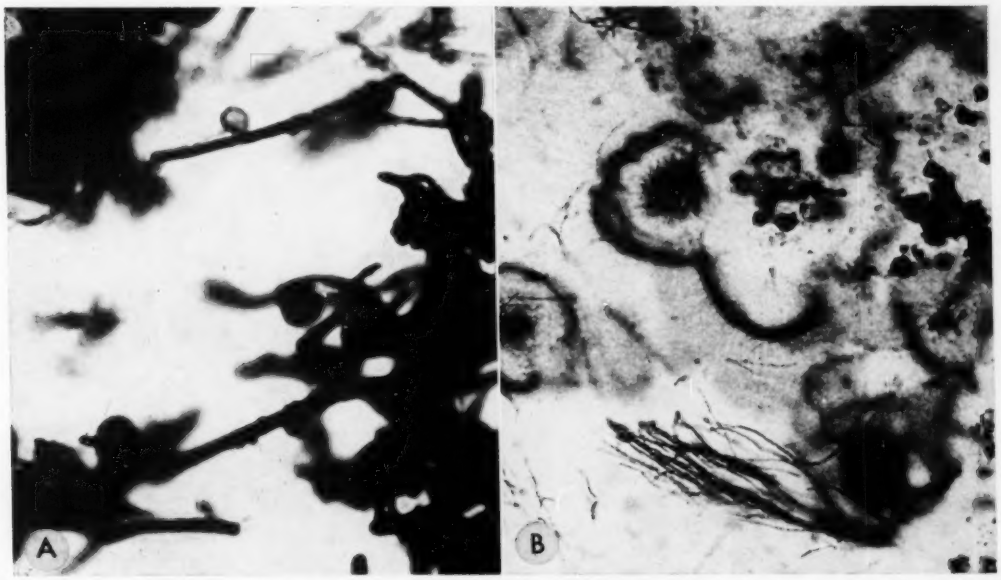

FIG. 17. The oldest known fossils. Pre-Cambrian plants of the Gunflint formation, Ontario, preserved in chert. A, fungus filaments and spores, × 750; B, algal filaments and spores, × 320 (Elso Barghoorn).

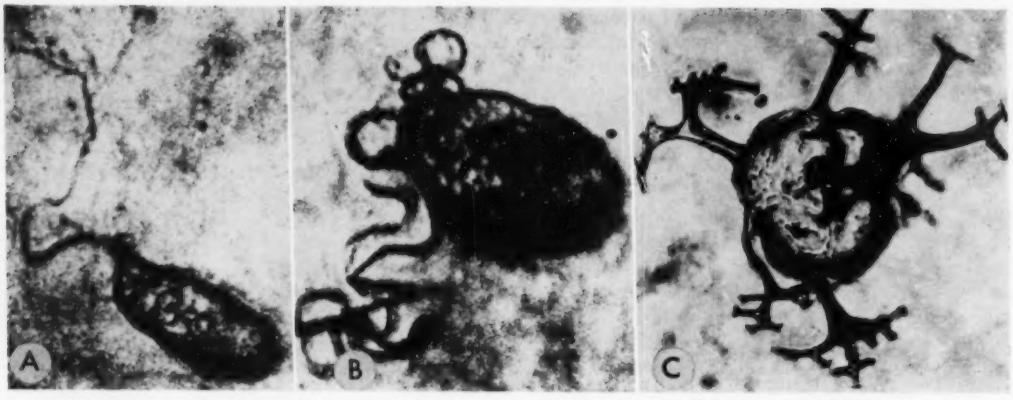

FIG. 18. Cretaceous flagellate protozoans in chert, Germany. A, euglenoid individual with flagellum, × 1,800; B, another individual with flagellum, × 1,055; C, hystrichospherid, × 700 (Wetzel, *Palaeontographica*, 1933).

they preserve traces of amino acids after 1,700 million years (fig. 17).

Until recently, the oldest known land flora was a lower Devonian peat bog, heavily impregnated with silica, found near Rhynie in the Scottish county of Aberdeen. Many species of beautifully preserved primitive vascular plants have been described from this locality together with the remains of many spiders, a mite, and a primitive wingless insect. Early Paleozoic protozoans (Chitinozoa) and graptolites are common in chert nodules. A great advance was made when Kozlowski discovered that many of these microscopic fossils are not appreciably altered from the original chitinoid condition and that they can be extracted from the hard matrix by means of hydrofluoric acid, which dissolves the silica but does not affect the fossils. Soft-bodied microscopic organisms, including the flagella of one-celled euglenoid forms, have been described in Cretaceous chert (fig. 18) in several well-documented reports by Wetzel (1933).

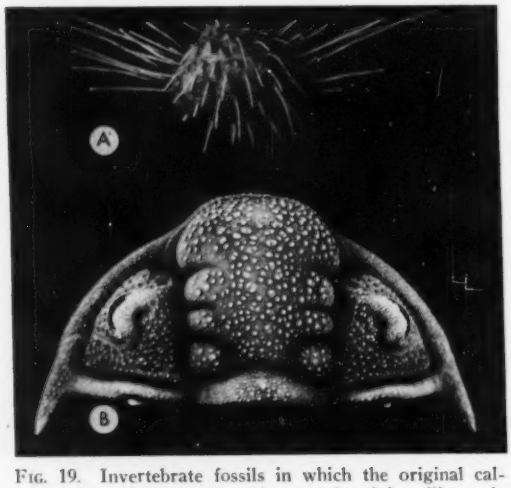

FIG. 19. Invertebrate fossils in which the original calcareous skeletons have been replaced by silica. A, spiny productid brachiopod, × 1, Permian, Texas (Cooper); B, trilobite, × 3, Ordovician, Virginia (Whittington, Geol. Soc. Amer., 1954).

CHEMICAL PREPARATION OF FOSSILS

Long ago, in the latter part of the nineteenth century, it was known that certain fossils may be extracted without damage from hard rock matrix by means of acids which either dissolve the matrix without harm to the fossils, or dissolve the fossils without affecting the matrix. In the latter case, the resulting cavity could be used as a mold to restore perfectly the external form of the organism or skeleton (fig. 21). Perhaps because of the relatively high cost of commercial acids in those days, this method of preparing fossils was never thoroughly explored until the past three decades. G. Arthur Cooper of the U. S. National Museum, more than any other, is responsible for an important revolution in paleontology through the development of "chemical" methods of preparation of fossils. In certain rock formations many of the calcareous fossils have been selectively replaced by silica. This was owing, presumably, to the catalytic effect of contained organic substances on silica-bearing solutions. The matrix commonly

was not affected by the replacement. Consequently, the more soluble rock matrix may be carefully dissolved away from the fossils with hydrochloric or acetic acid. Cooper has combined the advantages of mass collecting with chemical preparation. From 30 tons of Permian limestone collected in the Glass Mountains of Texas, he has extracted three million individual invertebrate fossils, almost all of which are exquisitely preserved with many delicate structures intact. The morphology of a large proportion of these fossils now can be worked out for the first time. A single control block of limestone weighing one hundred and eighty-six pounds yielded ten thousand excellent specimens of invertebrates, including Foraminifera, brachiopods (fig. 19A), bryozoans, gastropods, and pelecypods. Only a very few of these fossils were exposed on the surface of the rock and none could have been completely cleaned of matrix by mechanical means. A whole new fauna of mid-Ordovician trilobites preserved in this way has been worked out by H. B. Whittington and others (fig. 19B).

Extraordinarily well-preserved, uncrushed insects and other small arthropods with the body hairs and appendages clearly visible and some of the internal organs preserved were discovered by Bassett in calcareous nodules of Miocene age in the Calico Mountains, California. Palmer (1957) discovered that many of the insects have been impregnated, or coated, with silica so that they can be extracted in all exquisite detail from the matrix by means of acetic or formic acid (fig. 20). This discovery points the way to systematic examination and chemical preparation of calcareous nodules from other formations and areas. Bradley (1946) discovered well-preserved micro-organisms of several kinds in fossil coprolites of Eocene age in Wyoming. The fossil faeces belonging to reptiles and mammals contained a profusion of intestinal saprophytes closely similar to those of living forms. In addition, one of the mammalian

FIG. 20. Perfectly preserved fossil insect impregnated with silica, a female midge in the pupa, Miocene, California. The fossil was freed with acid from a calcareous nodule similar to figure 20C. A, posterior end of midge showing genitalia and body hairs, × 150; B, ventral view × 50; C, a typical calcareous nodule similar to that in which the fossil occurred, × 1 (Palmer, U. S. Geol. Survey, 1957).

FIG. 21. A nearly perfect restoration of a fossil amphibian prepared by dissolving the bones with acid from relatively insoluble rock matrix. The resulting natural molds of the individual bones were then used to cast replicas. The skeleton is about 5 feet long. A, original in matrix; B, reconstructed cast, Permian, New South Wales (Swinton, Brit. Mus. Nat. Hist.).

coprolites contained large numbers of fresh-water algae. The bacteria and algae are preserved in silica and show fine structures in detail.

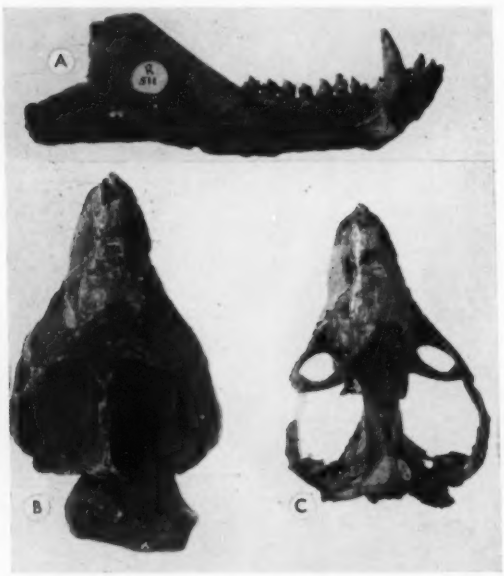

FIG. 22. Fossil skull of mammal-like reptile freed from rock matrix by softening and dissolving away the rock with acid. Triassic, South Africa. The skull is about 3½ inches long. A, nearly perfect jaw; B, original fossil before preparation; C, cleaned skull (Swinton, Brit. Mus. Nat. Hist.).

Calcium phosphate, the principal substance of vertebrate bones, conodonts, and certain brachiopods is nearly insoluble in acetic and formic acids which can, therefore, be used to dissolve calcareous matrix from these fossils. Many delicate and complex structures have been perfectly cleaned of hard matrix by this means (fig. 21). Usually the matrix contains much insoluble material so that chemical preparation must be supplemented with manual cleaning under a microscope.

SUMMARY

The known fossil record is characterized by systematic deficiencies as pointed out long ago by Charles Darwin; but as a record of preservable lowland and aquatic organisms, it is rich beyond the most optimistic predictions of nineteenth-century paleontologists. As collecting continues, it is becoming evident that the unsampled record in the rocks far exceeds the known record. Well-preserved fossils of some groups are abundant, and it may be confidently asserted that new discoveries made possible by new techniques of collecting and preparing fossils will necessitate revision of many present concepts about past life; but most of the revision will pertain to details of phylogeny and the accommodation of new categories not yet discovered. Many early generalizations about the record, the broad outlines of the history of many of the major groups, have been independently tested and confirmed many times.

These generalizations will not be so much affected by future discoveries.

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ANATOMY AND MORPHOLOGY: CLASSIFICATION AND EVOLUTION: 1859 AND 1959

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(*Commemoration of the Centennial of the Publication of* The Origin of Species *by Charles Darwin, Annual Meeting of the American Philosophical Society, April, 1959*)

Until an evolutionary *principle* was demonstrated, further random research could but swell the accumulation of data which awaited integration into a science. In this inchoate state anatomy remained until it was quickened by the publication of the *Origin of Species*, which forthwith raised this uneventful record of factual competence to the dignity of a learned discipline.—F. J. Cole

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INTRODUCTION

THIS contribution to our symposium is essentially a gloss on a single chapter in *The Origin of Species*, the chapter entitled "Mutual Affinities of Organic Beings: Morphology: Embryology: Rudimentary Organs."[1] In that chapter Darwin was primarily concerned with showing that the data on the subjects named provide strong evidence for the general theory of evolution. He was, however, also discussing the impact of evolutionary interpretation on understanding those data, and this is the more interesting aspect to us now. In order to understand that impact and its later results, we must have some idea of the status of the subjects when Darwin wrote and for some time before. In sketching in that background, I shall not be concerned so much with the priority or origin of Darwin's ideas as with the general climate of opinion in which he worked and which he so profoundly changed. Then after explaining, still necessarily in broad terms, Darwin's immediate influence, I shall try to show how the subjects have developed since 1859, how Darwin's ideas have fared and how these fields of study stand at the present time. Separate consideration is given to the two main topics, first morphology and then systematics, even though they are almost inextricably linked together and even though that was not Darwin's sequence.

Nowadays, among nonpaleontologists, at least, most work in systematics (including taxonomy and classification) is largely concerned with species and intraspecific populations. I shall, nevertheless, have little to say on that subject, first because Darwin discussed it only in passing in this particular chapter, and second because it will doubtless be emphasized in other contributions to this symposium. Another possibly surprising omission is that I shall have nothing to say about natural selection, and hence about Darwinism as it is usually strictly defined. That, too, is covered elsewhere in the symposium, but the reason for omitting it here is that it is not pertinent. The impact of evolution, and of Darwin, on these subjects of morphology and of systematics is almost independent of the possible mechanisms of evolu-

[1] Chapter XIII in the first edition (Darwin, 1859); chapter XIV in the sixth edition (Darwin, 1872). There are considerable differences between the first and last versions of this chapter, but most of them are insertions of additional examples and discussions. The arguments pursued and the principles expounded have few essential changes. In general I shall be referring to the first edition, because its anniversary is the occasion for this symposium and because in some respects it is superior to later editions. I shall have some occasion to compare the first and last (sixth) editions, but shall not attempt to specify the exact edition in which changes were introduced.

tion, such as natural selection. Darwinian and later evolutionary morphology does conclude (as a rule) that structural change is usually adaptive, but it has little closer connection with natural selection. It is further evidence of Darwin's genius that he did so greatly influence and advance whole fields of biological thought quite apart from the specifically Darwinian theory. There is a great deal more to Darwin's contribution than natural selection, and much that would hold up even if the selection theory were discarded.

I. ANATOMY AND MORPHOLOGY

FROM ANATOMY TO MORPHOLOGY

Sciences tend to go through an ontogenetic sequence: first, descriptions of separate phenomena, then comparative studies of groups of phenomena, then higher-order generalizations as to relationships among phenomena; finally (and this, too, commonly in a more or less complex sequence of its own), explanations of those generalized relationships. With the usual overlapping of precursors and laggards, anatomy went through the first three stages before Darwin. It was his remarkable feat to take it into the fourth stage, almost single-handed and almost at one leap. Of course the earlier stages, which provide the actual data for later stages, are not abandoned as the science progresses. The task of descriptive anatomy of single organisms is still in progress, and very far from complete, even now that theoretical anatomy is at an advanced explanatory level.

Belon's famous comparison of the bones of a man and of a bird (Belon, 1555) is generally taken as the beginning of comparative anatomy. He noted that the bones correspond, by and large, in the two species, and so he had a glimmering of the first and greatest generalization of anatomy: the principle of homology. It was, however, a feeble glimmer at best. Comparative anatomy grew up slowly in the seventeenth and eighteenth centuries. Most studies of animal anatomy [2] were not truly comparative, however, and were pursued almost entirely in the hope of throwing light on human anatomy. (There is an interesting parallel with the so-called comparative psychology of a far later date, which often consisted of studies on single species of animals, especially rats, in the hope of learning something about humans.) As late as 1753 Daubenton, one of the greatest developers of truly comparative but mainly descriptive animal anatomy, complained with justice that the study followed no philosophical system.[3]

The transition from descriptive anatomy to morphology,[4] a science with at least one principle, may be considered as coinciding with development of Belon's idea of equivalence between parts of different species. The use of animal anatomy as an adjunct to human anatomy was, indeed, based on belief in thoroughgoing equivalence—a belief not always justified. Naturalists soon came to recognize anatomical correspondences not only between man and (other) animals, but also among different kinds of lower animals and even among all animals whatsoever. The supposed correspondences were described in various terms, but often as "analogies" (e.g., Severino, 1645; Grew, 1681). Severino recognized four kinds:

1. Between different major groups (genera, a broader term then than now); e.g., lungs in terrestrial and gills in aquatic animals.
2. Between a major group and a minor group (species, also then broader); e.g., the eyes of vertebrates and the sensory tentacles of a snail.
3. Between two minor groups (species); e.g., hands or feet in monkeys and men.
4. Between parts of one species; e.g., hand and foot in man.

The distinction between 1 and 2 does not now seem wholly clear or important. The correspondence is inexact, but 1 and 2, together, 3, and 4 do roughly correspond with three categories still in use. The modern terminology stems, with considerable evolution of meaning, from Owen (1843), although, as noted, the basic concepts were much older and even the terms were not original with Owen. Owen restricted the old, general term "analogue" to "a part or organ in one animal which has the same function as another part or organ in a different animal" (Severino's examples under 1 and 2 belong here). He redefined the less well-known term "homologue" to mean "the same organ in different animals under every variety of form and function" (which includes Severino's

[2] The subject flourished as "zootomy" ("zootomia" of Severino, 1645), often contrasted with "anatomy," i.e., human anatomy.

[3] For the early history of comparative anatomy see the excellent book by Cole (1944), which, however, ends just when the subject is becoming most interesting. Zimmermann (1953) gives much material on the same period and later, through Darwin.

[4] The term "morphology" is much later, probably dating from Burdach (1810), and even then not quite in the modern sense.

examples under his 3). The adjectival forms "analogous" and "homologous" and the nouns "analogy" and "homology" for the relationships or principles are of course also in common use. Correspondences like those of Severino under 4 were later called "serial homology" by Owen, as further discussed on a later page.

IDEALISTIC MORPHOLOGY

Generalizations of a still higher order and an approach—although an abortive one—toward explanatory theory were sought by a series of naturalists who have been variously labeled "idealistic morphologists," "nature philosophers," "typologists," "transcendentalists," and "romantics." Among the leaders of this school were Goethe (1749–1832), Oken (1779–1851), and Owen (1804–1892). There were also many others and, indeed, virtually all nineteenth-century (and not a few twentieth-century) naturalists, systematists, and anatomists were influenced to greater or less extent by typological ideas. The main tenet is that the correspondences, essentially Owen's homologues, among organisms constitute an idea in the sense of Plato, a plan or pattern (*cf.* ὅμοια of Aristotle), or in this special sense a *type* which is common to the organisms in question. The type is a mental construct, but there is often a more or less clear claim that it corresponds to some transcendental reality or even that it *is* the reality of which the objective organism is only a sort of Platonic shadow.

In their more extreme forms such opinions become sheer mysticism. For instance there was a view—surely one cannot call it a theory—that there is really only one animal. Sometimes the one animal is specified as man, not, of course, any one or all of the objective individuals of our species but the "idea" or "type" of mankind. Tangible men are relatively complete manifestations of that ideal universal animal. "Other" (in quotes because they are "really" all one) animals are distorted and less complete manifestations of the same thing, if "thing" is the word. As with most other exponents of mysticism, these morphological mystics leave me completely baffled as to what they are talking about, and I therefore conclude that they are not saying anything. I am, in any event, quite sure that what they may be saying is not science and may be ignored in scientific enquiry.

The greater figures of the school of idealistic morphology, such as Goethe, Oken, and Owen, avoided the excesses of out-and-out mysticism. It is, nevertheless, difficult or (to me, at least) often impossible to gather what they really thought about the "type" or (in much of Owen's work) "archetype." Was it merely a mental construct, wholly and frankly artificial or subjective, but useful in describing, comparing, and classifying groups of animals? Doubtless such was the case for many typologists, especially those primarily engaged in classification, a subject to which we will return. Was it construed as some kind of transcendental reality? It was by the frank mystics. We have decided to ignore them, but almost the same sort of vague and inexplicable notion also seems tacitly to underlie much of the work on the subject by Owen and some other generally sound scientists. Was the type or archetype the plan, the blueprint so to speak, used by God in the creation? Certainly it was so for some pious naturalists, and even the not particularly pious Owen, especially in some of his pre-Darwinian work (e.g., 1849), seems rather plainly to hint, at least, that such was his concept. This is complicated but not necessarily contradicted by the fact that Owen also equated his archetypes with the ἰδέαι of Plato as eternal prototypes or preexisting molds into which matter was poured. Doubts are raised, however, by such later statements as that, "by the word 'creation' the zoologist means 'a process he knows not what'" (Owen, 1858).[5] In line with his idealistic morphology, Owen (1847) came to distinguish "special homology" (that of 1843, noted above) from "general homology," defined as the relationship "in which a part or series of parts stands to the fundamental or general type."[6]

Owen's definitions, and the usage of centuries before 1859, raise questions that were not entirely

[5] Still later Owen claimed that he had anticipated some of Darwin's ideas on evolution and natural selection, and yet he also paradoxically rejected Darwin's conclusions. His published works, as far as known to me, give no basis for his claims of priority. It is hard to avoid the conclusion that Owen was jealous of Darwin and wanted to discredit him in any way possible. The situation was doubtless more complex. A detailed study of the development of Owen's ideas would be fascinating and undoubtedly enlightening.

[6] At that time he also distinguished "serial homology," among members of a series of parts in a single animal, for instance arms and legs or successive vertebrae. In spite of some contrary opinions (notably Moment, 1945), serial homology seems to me a totally different phenomenon from special homology, or homology in the usual sense. It is not pursued further here, but is mentioned in the subsequent discussion of the vertebrate skull.

clear at that time and that were not answered until *The Origin of Species*. What is meant by "the same organ" and by "another part or organ"? Owen did find something disturbing in the latter expression, at least, for he later (1866, after publication of *The Origin of Species*) replaced "another" with "a" in the definition of "analogue." This made "analogue" and "homologue" not mutually exclusive but widely overlapping. Of course the "same" organ—whatever "same" is taken to mean—usually has the same function in different animals. Hence analogues, in Owen's final usage, are usually also homologues, and the emendation increased the ambiguity of the terms. Owen (1848) proposed that homologies (which is to say "samenesses") be judged by "the relative position and connection of the parts" and by "a close general resemblance in the mode of development," but emphasized that the latter is subject to modification and also that "form, proportion, substance, [and] function" do not determine homology. In bald words those suggestions are also extremely ambiguous, for how does one further define, for instance, "a close general resemblance"? They did leave many undecided instances, but in the practice of a skilled, one might say an intuitive, anatomist they worked surprisingly well. Yet all this left wide open the sense in which parts of two distinct species can be called "the same."

The step represented by Owen's definitions of homologues and analogues involves "higher-order generalizations as to the relationships among phenomena" (see beginning of this section). Thus the third stage in the development of comparative anatomy had been reached by 1843 (or well before that, but not so clearly). Yet the concepts of homology and analogy, as of 1843, are completely without explanatory content. They do not at all help us to understand the relationships that they specify.

The concept of types as eternal $\epsilon\tilde{\imath}\delta\eta$ or preexisting molds, still more as the blueprints of creation, does have an explanatory tinge. At least it refers the morphology of organisms back to an earlier cause or basis. It does not explain how archetypes originated (they are either eternal or of a divine origin hidden from man). It does not explain why they are what they are, short of a teleology unacceptable to both modern science and philosophy. And, incidentally, it does not tell us concretely how they may be recognized. It is still an explanation, or perhaps only a pseudoexplanation, by appeal to the unknown, as Owen on occasion frankly stated. The method of science can accept no explanation by appeal to the unknown if an explanation by the known is demonstrably possible. It was Darwin who demonstrated that possibility.

HOMOLOGY IN THE ORIGIN OF SPECIES AND AFTER

Darwin said of morphology, "This is the most[7] interesting department of natural history, and may be said to be its very soul." He recognized that morphology is mainly concerned with the study of types and homologues (using those terms), and went on to ask:

> What can be more curious than that the hand of man, formed for grasping,[8] that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include the same bones in the same relative positions?

After giving further examples, Darwin proceeded to justifiable criticism of some current ideas:

> Nothing can be more hopeless than to attempt to explain the similarity of pattern in members of the same class by utility or by the doctrine of final causes. The hopelessness of the attempt has been expressly admitted by Owen in his most interesting work on the *Nature of Limbs*. On the ordinary view of the independent creation of each being, we can only say that so it is—that it has so pleased the Creator to construct each animal and plant.[9]

Darwin had already remarked, in discussing classification earlier in the chapter, that characters

[7] With slightly tempered enthusiasm, he later (e.g., Darwin, 1872) revised this to "one of the most." Quotations without other citations are from Darwin (1859).

[8] Note that ". . . for grasping" and the following ". . . for digging" are teleological expressions, in spite of the fact that Darwin was engaged in refutation of the primitive teleology then still current. Darwin was necessarily using the vocabulary of the naturalists of his day. He might, however, have justified the usage by the fact, quite clear to him, that man's hand *is* for grasping and a mole's forefoot for digging in the sense that through natural selection they have evolved with respect to these functions in the economies of the two species. Without using Darwin's examples, Pittendrigh (1958) has discussed this justified kind of teleology, which he proposes to call "teleonomy."

[9] Later Darwin (1872) still more clearly recognized and stigmatized the creationist typological point of view, revising the last phrase to read: "That it has pleased the Creator to construct all the animals and plants in each class on a uniform plan; but this is not a scientific explanation."

common to members of a group [that is, their type, in the natural philosophers' sense] are due to "propinquity of descent." Now he goes on to amplify:

> The explanation is manifest on the theory of the natural selection of successive slight modifications. . . . In changes of this nature there will be little or no tendency to modify the original pattern, or to transpose parts . . . . If we suppose that the ancient progenitor, the archetype[10] as it may be called, of all mammals, had its limbs constructed on the existing general pattern, for whatever purpose they served, we can at once perceive the plain signification of the homologous construction of the limbs throughout the whole class.

In other words, homologous characters among organisms are those that they have received, through inheritance, from a common ancestry. In principle it is as simple as that! Darwin does not even feel the need to expand much on the flat announcement, which at once makes everything seem obvious. In his autobiography Darwin (Barlow, 1958) remarks that "innumerable . . . facts were . . . in the minds of naturalists ready to take their proper place as soon as any theory which would receive them was [proposed]." Facts about homology, innumerable indeed, had been accumulating for three centuries since Belon, and in 1859 they suddenly fell into place, took on new meaning, and were explained.[11]

Owen had distinguished, although not clearly or absolutely, two kinds of anatomical resemblances: homologues and analogues. Darwin explained one of these as due to common ancestry. (What he made of analogues is further discussed below.) In so doing, he implicitly provided a theoretically objective criterion as to what is and what is not a homologue. The common ancestry that not only explains but in this view also defines homologues did objectively exist if evolution is true. Some later authors (e.g., Boyden, 1947) have insisted that Owen's criteria are more objective and Darwin's merely subjective. This is curious because many of the *data* of both, the anatomical resemblances, are identical, and the additional data (mainly paleontological) pertinent to Darwin's definition are equally observational. The criteria for interpretation of those data were completely subjective for Owen: what constitutes "essential structural similarity" can only be subjective or intuitive. It is not even an opinion *about* a definable reality, which judgment of common ancestry is, at worst.

Although that argument really seems superfluous, there was an unfortunate semantic problem in the fact that Darwin's *explanation* of homology was implicitly also a *definition* (different from Owen's) and slowly came to be explicitly so recognized. Lankester (1870, 1907) observed the inherent difficulty and proposed to replace the initially ambiguous term "homology" by "homogeny," defined from the start as the relationship between "structures which are genetically related, in so far as they have a single representative in a common ancestor." For structural resemblance *without* that genetical connection he coined the term "homoplasy," although he was at first quite confused as to the dichotomy involved. (On the history of these and allied terms, see Haas and Simpson, 1946.) It might have saved some useless polemics if Lankester's terminology had caught on, but it did not. There is now extremely little disagreement in usage: "homology" is practically always understood to be *defined* by common ancestry, and "homogeny" has become an unused synonym of "homology." When usage is as nearly unambiguous as this is, there is no sensible arguing with it, and the fact that Owen or others before him did not thus define "homology" has only historical interest with no real bearing at all on present definitions.

A more fundamental minority objection to the current usage of "homology" was raised by Braun (1875) and has been repeated in almost identical terms by a few later writers. "Nicht die Deszendenz ist es, welche in der Morphologie entscheidet, sondern umgekehrt, die Morphologie hat über die Möglichkeit der Deszendenz zu entscheiden." Therefore, the argument runs, the concept of homology through common ancestry has no actual application in morphological research except, perhaps (and Braun denied even this), in the extremely few instances where the common ancestor is reliably known from fossils. A full discussion of this profound misunderstanding is not possible or needed here. We need only observe that the

[10] By deliberate use of Owen's term, Darwin is explicitly equating the hitherto idealistic, even mystic "archetype" with the real, objective common ancestry of the group in question.

[11] This is not meant to claim that no one before Darwin had any inkling of the evolutionary explanation of homologies. Absolute priority in scientific discoveries hardly exists or is, at any rate, unprovable. Darwin's statement was at least far more explicit and convincing than any earlier hints known to me, and general acceptance of this explanation of homology certainly stems from Darwin, which is the essential point here.

data are the same whether one is seeking, on one hand, "innere Zusammenhang" (Braun), "essential nature" (Blackwelder and Boyden, 1952), and the like, or, on the other hand, the genetical results of common ancestry, and that in both cases equally a mental inference or induction as to relationships among the data is necessary. Regardless of whether the actual phylogenetic lineage is known, the overwhelming majority of modern morphologists find that inference as to common ancestral origin is as practicable as and far more enlightening than inference as to "essential nature." [12]

AN EXAMPLE: THE VERTEBRATE SKULL

The rise of the various typological schools of morphology was intimately connected with the vertebral theory of the skull. According to this theory, independently conceived by Goethe and by Oken, the skull is a series of vertebrae with parts modified for functions distinct from those of the more posterior vertebrae. Thus Goethe (1820) wrote:

> . . . Ich denn . . . nur kürzlich meine vieljährig gehegte Überzeugung wiederhole, dass das Oberhaupt des Säugetiers aus sechs Wirbelknochen abzuleiten sei. Drei gelten für das Hinterhaupt, als den Schatz des Gehirns einschliessend und die zarten Lebensenden, fein verzweigt, in und über das Ganze und zugleich nach aussen hin versendend; drei hinwieder bilden das Vorderhaupt, gegen die Aussenwelt sich aufschliessend, sie aufnehmend, ergreifend, erfassend.

"Abzuleiten" is of course to be understood in an idealistic typological, not an evolutionary, sense. It denotes derivation from a transcendental pattern, not from a material ancestor.

This theory was widely accepted, notably by Owen (especially 1866). His illustration of the ideal archetype of the vertebrate skeleton shows the skull and jaws as a series of vertebrae (along with annexed bones: ribs, gastralia, etc.). All three of Owen's usages of "homology" are here involved and illustrated. The relationship between the archetype and any one real skull is his "general homology." Identification of bones in two different (real) species as both representing, say, the centrum of the supposed third cranial vertebra is "special homology." The relationship of the supposed cranial vertebrae and of their several parts to the more posterior vertebrae and their parts is "serial homology."

T. H. Huxley (1859) devoted a famous Croonian lecture to demolishing the essence of this theory. He asked, first, whether vertebrate skulls in general do show evidence of a common basic pattern. He answered "Yes," largely on embryological evidence of developmental similarities in skulls of widely different vertebrates. He then asked whether this basic pattern is identical with that of the vertebral column, and demonstrated most conclusively that it is not.

In *The Origin of Species* Darwin wrote:

> Naturalists frequently speak of the skull as formed of metamorphosed vertebrae . . . but it would . . . probably be more correct, as Professor Huxley has remarked, to speak of both skull and vertebrae . . . as having been metamorphosed, not one from the other, but from some common element. Naturalists, however, use such language only in a metaphorical sense. . . . On my view these terms may be used literally.

This statement and its context may be reexpressed for modern readers as follows: There is some kind of serial correspondence between skull and vertebrae. This goes back in a literal, objective way to a remote ancestry in which neither skull nor vertebrae existed, as such. Since then, the skull and vertebrae have evolved separately, each adapted by natural selection to their quite different functions. It is therefore misleading or perhaps meaningless to speak of serial homology between the skull and the vertebrae of an animal in which those specialized structures have already evolved.

That understanding of the matter is still completely acceptable to modern morphologists. Huxley (perhaps given undue credit in Darwin's statement) quite failed to see the "common element" of which Darwin wrote, because he denied that the cranium ever "becomes segmented into somatomes" in embryological development. In fact it does, as was then already suspected, and has since been throughly demonstrated (e.g., Goodrich, 1930; de Beer, 1937). This segmentation into somites, still preserved in vertebrate embryos, is clearly inherited from the metamerism of a prevertebrate ancestor, and that metamerism is Darwin's "common element."

[12] It is beside the point that inference about common ancestry, like any other scientific induction, may be mistaken. To be sure, Owenian inference about the "sameness" of structures may never be mistaken, because it is an opinion unrelated to anything objective in nature, and it must generally be true that a stated opinion *is* the author's opinion.

Embryological evidence, which figures so largely in final understanding of the vertebrate skull, was discussed at some length by Darwin in the chapter here under consideration. He knew that embryos of related animals often resemble each other more than do adults and correctly explained this by noting that earlier ontogenetic stages may be less modified in the course of evolution. It follows, as Darwin also noted, that embryos may more nearly preserve ancestral characters and that homologies may be evident in them although obscure in adults. He mentioned, almost wistfully, the possibility that embryonic stages may resemble the adults of earlier animals, but regarded this as unproved and perhaps unprovable. In general his interpretations are in terms of the evolution of embryological development, avoiding the errors and excesses inherent in the later catch phrase "ontogeny repeats phylogeny." [13]

Since Darwin the evolution of the skull (and jaws) and the homologies of its various bones among the classes of vertebrates have been intensively studied. As far as homologies are concerned, these have been almost completely traced among the tetrapods (amphibians, reptiles, birds, mammals), largely from the now abundant fossil materials. The most extraordinary result of this work is doubtless the now familiar homology of the amphibian and reptilian articular and quadrate with, respectively, the malleus and incus of mammals. It is, incidentally, difficult to see how any idealistic theory of "essential resemblance" or "nature" could encompass such a change in type, which is beyond any doubt as an evolutionary homology. Among the fishes, and especially among the earliest fossil aquatic vertebrates, the homologies of skull bones are still frequently uncertain. This is a very active and somewhat controversial field of investigation at the present time, especially among Stensiö and his followers in Sweden and Watson and his in England.

The history of investigation of skull morphology has been interestingly given at much greater length and with many illustrations and references by Peyer (1950), in a monograph that covers much more ground than its title—*Goethes Wirbeltheorie des Schädels*—suggests.

[13] In 1859 Darwin was curiously ignorant of the crucial prior work by von Baer, but he corrected this oversight in later editions. It was largely Darwin who eventually put von Baer's nonevolutionary embryology into an evolutionary framework. The misleading interpretation of the so-called biogenetic law was mostly due to Haeckel. For a modern summary of evolutionary embryology see de Beer (1951). Important as it is, the subject cannot be pursued further in this limited essay.

NONHOMOLOGICAL RESEMBLANCES

It has been indicated that many morphologists, from the eighteenth century on, recognized that there is more than one category of resemblances among organisms. They did not, however, achieve clear-cut definitions of such categories or, at least, definitions that most modern morphologists would find satisfactory. Owen's contrast of homologues and analogues was perhaps the best before Darwin but still was not adequate. Aside from the problem of subjectivity or intuition in recognizing what are and what are not the "same" organs, the terms overlap because, as has been noted, in Owen's later usage (e.g., 1866) the same organ was generally *both* homologous and analogous to an organ in other animals.

In Darwin's work and that of most morphologists after him homology is resemblance due to inheritance from a common ancestry. What, then, of the other member of the logical dichotomy, resemblances not due to that cause? Darwin seems, indeed, to deny that such resemblances exist, for he writes of "propinquity of descent" as "the only known cause of the similarity of organic beings." That is, however, a paradox, a contradiction of himself perhaps from enthusiasm, shifting of emphasis, semantic reservations, or even simple oversight (although he left the paradoxical statement in all editions of *The Origin*). In fact he had something to say about resemblances not due to "propinquity of descent" in the first edition and subsequently largely expanded this. In 1859 Darwin wrote:

> We can understand on these views, the very important distinction between real affinities and analogical or adaptive resemblances. Lamarck first called attention to this distinction. . . . The resemblance, in the shape of the body and the fin-like anterior limbs, between the dugong, which is a pachydermatous animal, and the whale, and between both these mammals and fishes is analogical. . . . Animals belonging to two most distinct lines of descent, may readily become adapted to similar conditions, and thus assume a close external resemblance; but such resemblances will not reveal—will rather tend to conceal their blood-relationship.

And he goes on to point out that the characters in which whales resemble fishes are "analogical" in that connection but that those same characters among the whales, alone, exhibit their "true af-

finity"—i.e., in that relationship they are homologues (a term Darwin does not use at this point but does later in the chapter).

In later editions (e.g., 1872) Darwin further stressed "striking resemblances in quite distinct beings between single parts or organs, which have been adapted to the same functions," and he gave the now widely used example of the [placental] dog and the [marsupial] Tasmanian "wolf." He noted further that, "In all such cases some fundamental difference in the growth or development of the parts, and generally of the matured structure can be detected: The end gained is the same, but the means, though appearing superficially to be the same, are essentially different." This is, of course, the now very familiar phenomenon of convergence.[14] Darwin did not use that term at this point, but he did use it earlier in the book (in chapter IV, in a passage also added after the 1st edition). There he is arguing against the suggestion (by H. C. Watson) that convergence could falsify classification by producing essentially identical forms from different ancestries. To this Darwin replied that, "It is incredible that the descendants of two organisms, which had originally differed in a marked manner, should ever afterwards converge so closely as to lead to a near approach to identity through the whole organism."

By 1872 Darwin also had inserted discussion of still a third kind of resemblances, due neither to "propinquity of descent" nor to being "adapted to the same function": mimicry. Conceptions of mimicry, especially, have become more complicated since Darwin's day but we still recognize his three kinds of resemblances, classified by evolutionary process as due to common ancestry, to adaptive convergence, or to mimicry. Those are the three main categories and perhaps the only ones, although there are other probably unimportant possibilities about which evolutionists do not now agree. Parallel mutations (nearly what Darwin meant by "analogous variation") doubtless occur, but most students now think they are unlikely to produce marked resemblances, at least, unless they are involved in *adaptive* convergence (or parallelism). Some resemblances may even lack causal explanation, by which I mean to say that the characters involved have separate causes and the resemblance is sheer coincidence, like the resemblance between moss and moss agate.

[14] Parallelism is also related to this subject and to Darwin's "analogous variations," but it is unnecessary here to discuss further these rather vague and abstruse distinctions. See Haas and Simpson, 1946.

Although Lankester's term "homogeny" for what nearly everyone now calls "homology" is obsolete, his term "homoplasy" is still in use. Lankester himself was not really clear, but it is now universally agreed that homoplasy covers all resemblances that are not homologous in the ordinary sense, that is, those not due to community of descent. "Analogy," also still current and in wider use than "homoplasy," is now generally understood to refer to resemblances not due to common descent (not homologous) but involving similarity of function. Most, but not all, present-day evolutionists use analogy, as they do homology but not homoplasy, in an explanatory sense. For them analogy not only involves but also is due to similarity of function, in the sense that adaptation to similar functions has produced the anatomical or other resemblances in question. Thus analogy and mimicry are two different special cases of homoplasy. (Again see Haas and Simpson, 1946.)[15]

Thus by evolution of terminology and systematization of concepts, the stock in trade of the modern evolutionary morphologist includes the following terms and concepts for what their seventeenth-century forerunners were calling analogies:

Homology (from common ancestry)
Homoplasy (similarity without homology; not from common ancestry)
Analogy (from adaptation to common functions)
Mimicry (close resemblance to other species or objects, not related to common functions but probably in all cases adaptive in one of several other ways)
—and probably others of less importance.

II. CLASSIFICATION AND EVOLUTION

KINDS OF CLASSIFICATION

Biology students are often bewildered by the fact that there are so many different classifications of the same organism. They want to know "Which is right?" When told that the question is meaningless, they may be inclined to go in for mathematics, where the right answers are in the back of the book, or literature, where the question of rightness does not arise. Those who do persevere in the more difficult study of biology learn that there are many different methods and criteria for classification,

[15] I feel sure that these usages of the terms follow a strong consensus and are the only ones that are now generally understood among biologists without explicit definition each time a term is used. There is, however, some dissent.

that a classification can be wrong if it contradicts its own principles, but that it can never be right in the sense of being the only one possible from a given set of principles. Furthermore there is no one set of principles that is inherently right and puts the others in the wrong, although it can be shown that some principles are better than others in a heuristic sense if in no other.

The principles of taxonomy may in theory, at least, be completely natural, and search for a natural taxonomy is the main theme in the history of this science. Classification, on the other hand, always and necessarily has a large element of artifice.[16] A classification may be completely artificial, as in old herbals and natural histories with plants and animals listed alphabetically by their names. That is a legitimate classification and the most convenient one possible if you want to find a description of an organism whose name you know. (It is therefore still widely used in dictionaries and encyclopedias, not to mention indexes of works on natural history.) It nevertheless obviously has nothing to do with nature. There is some connection with nature in the classification of organisms by their uses, also common in herbals, and still more in classification by habitats, of great antiquity and now revived in ecological and zoogeographical studies.

Even classification by uses or habitats is not what taxonomists have meant by "natural classification." In fact the long search for natural classification was marked precisely by attempts to get away from any such criteria external to the organisms being classified and to classify them on their own inherent qualities. All other systems of taxonomy are characterized (not necessarily stigmatized) as "artificial." It is, further, artificial taxonomy in the usual understanding of the words to classify organisms by their own characters if these are selected only for their convenience in identification. For instance the successive specification of an animal with wings, with two legs, without teeth, living in western United States, colored blue, six to eight inches long, leads to positive identification of *Sialia currucoides*.[17] Every specification is certainly of a natural characteristic, but at every step that sequence establishes groups that no taxonomist today or for several centuries past would call natural. What, then, is a natural classification? Darwin's answer to that question was his major contribution to taxonomy.

[16] There is no general agreement on definitions of the three terms most pertinent to this subject: systematics, taxonomy, classification. Some use all three or at least the latter two as if they were synonymous. There may not be a consensus, but there is respectable authority for adopting the following distinctive definitions. Systematics is the study of the diversity and, in the broadest sense, the relationship of organisms. Taxonomy is the study of the principles or theoretical bases of classification. Classification is a formal arrangement of the kinds of organisms in various groups and the application of symbolic designations to (or the nomenclature of) the groups recognized. Thus classification is a concrete application of taxonomy and both classification and taxonomy are included in the broader subject of systematics.

THE BASIS FOR NATURAL CLASSIFICATION

An intuitive feeling for the natural grouping of animals dates from antiquity, doubtless from prehistory. At that level it appears in most vernaculars. For example, we recognize the affinities of a considerable number of visibly different species by calling them all "squirrels." But neither in common speech nor (unless we are somewhat sophisticated in natural history) in usual thought do we recognize that a ground hog is also a species of the same general group. A ground hog resembles squirrels closely in many respects, but differs from them markedly in others. Intuitive or folk perception has passed over the resemblances and selected the differences as definitive. The example is naive, but the most scientific taxonomist has to go through the same process at a different level. Between any two organisms there are resemblances and differences. A natural classification—whatever is meant by "natural"—must evaluate these, and to evaluate them scientifically there must be some theoretical basis for the evaluation.

Early naturalists divided plants into trees and shrubs and placed frogs and beavers in the same group because they are both amphibious. Even in the seventeenth century more advanced students felt that such groupings were "wrong"—unnatural in some way—although Ray (1693) still classified whales as fishes. Ray, in most respects remarkably advanced, was much concerned with the search for a natural system. He concluded that a natural group is defined by a common structural plan (Aristotle's ὅμοια). (The close connection with the development of typological

[17] This is, of course, an exaggeratedly artificial example of key classification, a method still in wide and effective use. Although admittedly artificial, keys can often be brought into fairly close correspondence with a natural classification and this is now usually attempted.

morphology is apparent.) In practice, of course, the problem is to define the plan, and this consists of the characters in common within a group. In short, the group gives the plan, the plan gives the group—a complete circularity from which pre-evolutionary typological taxonomy never was able to free itself. On his own grounds Ray's classification was readily defensible, for there is a whale-fish common plan as well as a whale-mammal plan, and there was no apparent reason for giving precedence to the latter.

Linnaeus, most renowned of all pre-Darwinian taxonomists, was also intensely concerned with achieving a natural system. In part his criteria were that it is more natural to classify by some organs than by others. He was, of course, famous for his natural system of plants based primarily on their sexual parts. As to *why* resemblances among some organs indicate more natural groups than those among others he provides no answer. His theoretical background was that of special creation of genera and species (although in later life he admitted some possibility of evolution *within* genera). Those units are, then, real in nature and so completely natural, *if* we can identify them. Higher categories were for him partly natural, partly artificial—in just what mixture or way is again obscure. Darwin quotes one of Linnaeus' famous aphorisms, that the characters do not make the genus but the genus makes the characters. In other words we do not know *a priori* what characters will define a group but observe them as common to the group once that is given (which is one side of Ray's circular procedure). In a more modern context this has become an essential taxonomic principle. As Darwin pointed out, it was ambiguous or insufficient as Linnaeus expressed it, because it implies that something *other than characters in common* makes the group, but does not say what that is.[18]

Ray and Linnaeus typify the great majority of taxonomists who classified by characters in common. That system implies a group-within-group structure of a whole classification. The closest visual symbolization would be by a series of circles of different scope. The largest circle represents the minimal numbers of characters in common, verbally symbolized simply as "organisms." Next within that circle are two smaller circles, coordinate with each other, representing plants and animals, with more characters in common within each than in the largest circle that includes both. Each of these circles again contains a number of coordinate circles, with still more characters in common, each representing a phylum. And so down the familiar hierarchy to circles of minimum size and maximal characters in common, representing species, subspecies, or local populations. In typological terms, each circle is a pattern or archetype, the largest circle being most general or with fewest details or elements in the pattern, the smallest circles most specific (in both senses), with greatest elaboration of detail.

That group-in-group plan was not the only formal pattern of classification involved in pre-Darwinian taxonomy. Many taxonomists felt that a natural classification should be linear, corresponding with the scholastic *scala naturae* and strongly implicit in the philosophy of Aristotle. In extreme form, such a classification has a single linear sequence like that of Bonnet (1745) which runs from man-orang-monkey . . . to . . . air-fire-subtler matter. In reaching this arrangement Bonnet followed three principles: (1) comparative complication or height of organization (man of course having the most and "subtler matter" virtually none); (2) continuity, the chains of matter including all beings but God and having an almost endless number of intermediates; and (3) linearity, the belief that there is only one chain.

Comparatively few accepted Bonnet's third principle. Cuvier, for instance, probably the most influential taxonomist of the early nineteenth century, was polemic against it, maintaining that the theory of a single sequence of beings had greatly hindered the progress of natural history (Cuvier, 1817). He proposed instead an essentially typological, group-in-group system with four main types ("plans" corresponding with the "embranchements" of the classification) of animals. In fact neither then nor later did the usual taxonomist make a really decisive distinction between the group-in-group and the linear classificatory schemes, and most classifications right down to the present time are influenced by both. One reason for this is that classifications are written and that it is impossible to write one name *within* another. In general one name follows another, and there is a linear element in any written classification even though it be considered an artifact. Group-in-group classifications usually represent grades in

[18] Yet Darwin's objection applies to practice rather than to theory, which is our main concern here. Linnaeus' belief was that God made the genus, which does not help to recognize it but does give it a theoretical definition.

the hierarchy by degrees of indentation. In a pure group-in-group scheme, it should be understood that names equally indented, corresponding with groups at the same level in the hierarchy, are all absolutely coordinate and that their sequence has absolutely no significance. Nevertheless, *they are* in sequence, and most taxonomists plainly do attach some meaning to the sequence. Classifications of animals to this day practically always begin with Protozoa and end with Vertebrata (which in turn begin with cyclostomes and end with mammals). Some taxonomists vehemently deny that this is a sequence from lower to higher (although students are usually told that it is). But even the most stubborn group-in-grouper never thinks of putting vertebrates, say, between protozoans and sponges. That seems inherently unnatural! In fact, Bonnet's first two principles are still widely accepted, even though understanding of them is now far more complex and more subtle.

The pre-Darwinian theoretical basis for a linear scheme, when any was given, was essentially the same for the typological group-in-group scheme. It was idealistic: The scheme was imposed by the eternal idea or pre-existing mold, or it was the pattern of creation. Such classification culminated with Owen, along with the idealistic or archetypal morphology that is so plainly related to it.

Lamarck (especially 1809) brought evolutionary concepts into contact with classification and thus pointed a way toward a radically different theoretical basis for taxonomy. The idealists frequently spoke of "natural affinities" among animals, but their concept of natural affinities, never really clear, was rather transcendental than natural. With Lamarck it became possible to give the term a really natural, material meaning: that of genetic relationship. Lamarck, himself, did not much advance the practice of classification, a comparative failure due largely to his philosophical adherence to the linear scheme. He believed thoroughly in all of Bonnet's principles, but he reinterpreted the supposed single linear sequence as a pattern inherent in life that organisms tended to follow in the course of their evolution. From such a basis it is hardly possible to develop new evolutionary criteria for taxonomy, because one must still make the practically impossible judgment as to the relative degree of perfection or complication of each organism and then insert it accordingly in the evolutionary scale. Lamarck found that he could not, in fact, arrange all organisms in one sequence. He supposed that the sequence had been perturbed by local adaptation independent of and superposed on the truly inherent linearity. When he came to draw up what we would call a phylogenetic tree—apparently the first ever published—he showed it as zigzagging and somewhat branching (Lamarck, 1809). In practice his recognition of groups was mainly typological.

Darwin accepted as a point of departure the group-within-group, hierarchical, characters-in-common, typological classificatory system most common in his day. But he refuted the idealistic, transcendental background, and he supplied a thorough-going evolutionary explanation. Starting with the observation of groups within groups ("groups subordinate to groups," in his words) he shows that these can be explained by propinquity of common ancestry. A broader group had a remote common ancestry ("parent"). An included or subordinate narrower group had, within the greater group, a less remote common ancestry. And so on down the hierarchy. He asks, in effect, what is natural about earlier "natural systems"? They become truly natural when groups are interpreted as united by the natural processes of reproduction and descent. He notes (as mentioned above) that Linnaeus' treatment of the genus requires "something more . . . than mere resemblance," and he avers that the something more is "propinquity of descent." Thus in principle the new, truly natural basis for classification is quite simple. The groups of a natural classification are composed of organisms of common descent. Their higher or lower (that is, more or less inclusive) place among the categories of the hierarchy will tend to be in inverse proportion to the propinquity of descent, or in direct proportion to the remoteness of the common ancestor. Actually, of course, there are many complications and difficulties in the application of these brilliantly simple concepts; Darwin was well aware of some of the worst of them, although he was, to be sure, somewhat overoptimistic, which is surely excusable.[19]

MORPHOLOGICAL CRITERIA IN THE PRACTICE OF CLASSIFICATION

In Darwin's day the characters used in the definitions of taxonomic groups were almost en-

[19] Zimmermann (1953) has made a very useful compilation of extracts and abstracts from pre-Darwinian authors, bearing on both morphology and classification. (For post-Darwinian authors the selection is less full and is poorly representative.) For an excellent example of successive classifications of the same group of organisms (mammals) see Gregory (1910).

tirely anatomical, and these still predominate although to significantly lesser degree. There is a frequently misunderstood but really not too difficult distinction between, on the one hand, classifying the *characters*, themselves, or classifying organisms directly by their characters and, on the other, using the characters as *evidence* that some ulterior standard is being met. Even today classifiers impatient with the theoretical subtleties of taxonomy sometimes say that a classification should be based simply and solely on degrees of anatomical (or other inherent) resemblance or on the total number of characters in common, without the introduction of any theoretical or "subjective" considerations. To anyone who has never really classified organisms [20] this may sound sensible and simple. In practice, however, both the facts of nature and the history of taxonomy show that such classification is completely impractical.

In the first place, it is absolutely impossible in the present state of techniques, at least, to determine *all* the characteristics of even one organism, let alone of all the countless billions that must be classified. ("Billions" is figurative and an obviously absurd underestimate if taken literally.) There is always a very stringent restriction and selection as to what characters can be and are actually used. To proceed without an acknowledged basis for such selection is surely unscientific, and about as subjective or merely intuitive as it is possible to be. Even if the impossible evaluation of total characters in common could be managed, the results would frequently be unsatisfactory. No one can say for certain, but it seems probable that the Tasmanian "wolf" and the placental wolf have more characters in common than the Tasmanian "wolf" and a kangaroo. But even the nonevolutionary taxonomists placed Tasmanian "wolf" and kangaroo in a group apart from the placental wolf, and no critic of phylogenetic classification has ever suggested doing otherwise. Moreover, it is quite common for a given group to have about the same number of characters in common with two, three, or even more other groups when it is hardly possible to base a rational or workable classification on such a complex of resemblances. A large-scale example is provided by Ameghino's attempts to base classification of extinct South American mammals on conflicting resemblances to groups themselves highly dissimilar. (See Simpson, 1948.)

Looked at from this point of view, the long groping after natural classification was precisely an effort to get away from strict characters-in-common methods and to find some canon for selection of those characters that could somehow be given predominance. Habit of growth, as between for instance a tree and an herb, is certainly the most striking single characteristic of a plant and was, as we have seen, given priority in some early classifications. It was nevertheless early abandoned as, in some undefined sense, an unnatural basic criterion. Linnaeus' (1735) "sexual system" of plant classification was an attempt to find more natural criteria. But that was still a completely arbitrary decision, as is evident by the fact that Linnaeus, himself, later (1763) proclaimed that leaves, not flowers, provide the most "natural" criteria for classification.

The problem was exaggerated as a strict typology became the vogue, whether or not it was accompanied by a transcendental, Platonic, or creationist theoretical background. You cannot abstract a type including more than one species unless some characters of each group (those in which they differ) are left out. Among, say, three species, *a*, *b*, and *c*, omission of some characters will put *a* and *b* under the same type, while omission of others will give a type covering *b* and *c* but not *a*. It is necessary to decide that some characters are important and others unimportant, and discussion of this problem has been widespread throughout the history of taxonomy. Cuvier (e.g., 1817), for instance, gave precedence to characters that are most constant (because, as he theorized, they fulfilled constant adaptive requirements of the conditions of life) and to those that are most important in the functioning of the organism. Both criteria were widely accepted and generally used in classification. Among characters supposed to be important in classification of animals because they are important to the animal, means of locomotion and of food getting were often mentioned. And yet other authorities reached exactly opposite conclusions, as when Owen implied that characters least related to habits and food were most indicative of "true affinities." How can one judge?

Darwin discussed these matters in some detail. He showed that his new taxonomic basis in propinquity of descent affords criteria for the importance of characters, and he also showed that in some respects these criteria are different from

[20] It is true that some of the proponents of entirely characters-in-common or simon-pure morphological classification are experienced and technically adequate classifiers. But an examination of their classifications shows that they do not practice what they preach.

those previously most widely used. He stressed that characters, such as those of locomotion and food getting, that are most related to the special habits of animals are likely to be of least importance for classification. On that point he agreed with Owen but Darwin had, and Owen lacked, an explanation. It is, on Darwin's view and ours today, just such specially adaptive characters that are likely to differ most from a common ancestry through which broadest, most basic affinities may be traced. It is also just such characters that are most likely to appear independently in groups adapted to similar ways of life but of different ancestral origins.

Darwin also emphasized, as did most pre-Darwinians and as any practical taxonomist must, the importance of characters that are constant through large groups of species and constantly absent in others. Yet the taxonomic value of such characters is not, as Cuvier and many others had believed, because of their physiological or functional importance. That is contradicted by the point already made of the low taxonomic value of many characters of special adaptive value, quite constant in and highly important to the groups possessing them but of little use in determining a more remote ancestry. It is further contradicted by the fact that the same vital characters may be constant in some groups and highly variable in others. For Darwin, the significance for classification of constancy of a character among many species had nothing to do with its physiological importance. The important thing is that such characters are most likely to have been derived from a common ancestry, and hence to be valid evidence for grouping the species together by propinquity of descent.

Darwin insisted that under his theory of taxonomy trifling and "rudimentary" (usually meaning what we now call vestigial) characters are of high value for classification. This is not in spite of but precisely because of the fact that their physiological importance is slight or nil. They are for that reason all the more likely to have persisted from a remote ancestry, while characters of more vital significance are more prone to change in adaptation to changing conditions in the course of evolution. Darwin further pointed out that the taxonomic importance of "trifling" characters, or indeed of almost any characters, is greatly increased if they are correlated (in fairly constant association) with other characters, even though (or we would say especially when) there is "no apparent bond of connection" among them. The reason is not, to be sure, quite explicit in Darwin's words but is plainly implicit in his whole discussion. Any one character may change quite radically in the course of evolution and become highly diversified even among related species, but if several independent characters remain associated in otherwise diverse species the chances are that they have been derived with little change from a common ancestry.

It is easy to show, and Darwin himself did show, that Darwin was anticipated by earlier taxonomists on almost any one of his criteria for the taxonomic importance of characters. On the point made in the last paragraph, for instance, de Candolle (1819) had argued that "the really natural groups" will be the same whether they are set up by one sort of character (e.g., vegetative parts of plants) or by another (e.g., reproductive parts) and that the association in practice is therefore a prime criterion as to whether a group is natural. The essential point about Darwin's views on criteria of classification is not whether each one was original or not. It is that he provided a consistent system by selecting among the many contradictory criteria previously suggested and explained why, under this system, the selected criteria are consistent and valid. No previous taxonomist can really be said to have done this.

THE PROBLEM OF CONTINUITY

There is one criterion of relationship that has a unique status in evolutionary systematics: the existence of transitional forms between groups. Bonnet's second principle, that of continuity, was widely but not universally accepted by nonevolutionists. As applied to recent organisms, at least, the principle is by no means general and has, indeed, vastly more exceptions than exemplifications. In groups that are, as we now put it, in or just past a phase of territorial and ecological expansion, with adaptation to varied environments and active speciation, there may indeed be essential continuity in the characteristics of subspecies of a species, species of a genus, or even genera of a subfamily or family. It is, however, decidedly the rule among species and genera and practically without exceptions among families and higher groups that there are quite definite discontinuities between groups of recent organisms. This was of course well known to Darwin's contemporaries and predecessors. It is fundamental in the bases of typological taxonomy, and it was also a major argument for special creation. The nonevolution-

ists who subscribed to the principle of continuity therefore could do so only in a vague and broad sense or as a philosophical ideal not realized in nature.

In imposing an evolutionary interpretation onto a linear system like that of Bonnet (and many others), Lamarck saw that the principle of continuity was crucial. He insisted that the limits between taxonomic groups, even those apparently best defined, are vague and said that the transitional series of taxonomic groups set up by classifiers are real in nature but the divisions between them are not. Nevertheless, when he came to discuss actual phylogeny (and corresponding classification) he recognized that there are great gaps in the series, for example between mollusks and fishes, two groups that he believed to be successive in the scale of nature. He could only postulate that the gaps would eventually be filled by forms "still to be discovered"[21] (Lamarck, 1809).

This problem has two aspects and Darwin discussed both of them in ways that are, in essence, completely acceptable today. First, he recognizes sequences or "chains" among recent organisms, and he contrasts the use in classification of the characters-in-common or group-within-group and the sequential or chain method. Using very broad examples, he says:

> Nothing can be easier than to define a number of characters common to all birds; but in the case of crustaceans, such definition has hitherto been found impossible. There are crustaceans at opposite ends of the series which have hardly a character in common; yet the species at both ends, from being plainly allied to others, and these to others, and so onwards, can be recognized as unequivocally belonging to this, and to no other class of the Articulata.

Most of Darwin's taxonomy, like that of almost everyone at the time, was essentially typological even after it became evolutionary. But here with his usual happy eclecticism he brings in a markedly different approach to classification which in the evolutionary context complements and does not conflict with the typological or characters-in-common approach. The evolutionary concomitants are not explained at this point, but are made clear in his discussions of phylogeny[22] elsewhere. Characters-in-common reflect a common ancestry that also had those characters, and the breaks setting off a given "type" (such as that of the Class Aves) are caused by extinction of intermediates. In a case like that of the crustaceans the whole group has evolved so far and has diversified so much that characters in common (and not also common to other classes) have disappeared, but *within* the group most of the divergent lines have survived and so have retained a "chain" of resemblances which is itself evidence of common ancestry.

The second and still more crucial aspect of the problem of continuity is that if evolution is a fact and if, as Darwin but not all evolutionists believed, it normally proceeds by slow and gradual changes, then the complete sequence of organisms, both living and extinct, would be absolutely continuous throughout. Natural classification of two contemporaneous groups as separate is possible only because we do not know their common ancestry or do not try to place it in the same classification. There is in Darwin's theory, accepted in this respect by a great majority of modern taxonomists, no natural separation between the contemporaneous groups and their common ancestry. After making this difficulty clear, Darwin concludes:

> In a [phylogenetic] tree we can specify this or that branch, though at the actual fork the two unite and blend together. We could not . . . define the several groups; but we could pick out types, or forms, representing the characters of each group, whether large or small, and thus give a general idea of the value of the differences between them. This is what we should be driven to if we were ever to succeed in collecting all the forms in any class which have lived throughout all time and space. We shall certainly never succeed in making so perfect a collection: nevertheless, in certain classes, we are tending in this direction. . . .

This passage again demonstrates that Darwin still thought of taxonomy primarily in typological terms, even though he so firmly rejected the idealistic and creationist concepts of types and even though he brought in some distinctly non-typological principles. The fact that even Darwinian typology is no longer acceptable (see below) has invalidated his over-simple solution of

[21] He meant undiscovered living intermediates, not extinct ones such as have, indeed, been found between many major groups. (Although not between mollusks and fishes!) Even though he was an evolutionist, Lamarck then shared with Jefferson and many others the belief that species never become extinct—a curious failure of insight, especially in view of the fact that the anti-evolutionist Cuvier accepted the already overwhelming evidence that many species have become extinct.

[22] The word "phylogeny" does not occur in the first edition of *The Origin of Species*. In later editions Darwin introduced the word, citing Haeckel.

the problem.[23] In fact no entirely satisfactory solution in taxonomic principle has yet been achieved. The whole subject seems to become more and more complex and has been much discussed in recent years, especially by paleontologists, who among taxonomists are most likely to encounter the problem in practice. On the other hand, in spite of the almost incredible increase in fossil collections since Darwin's day, there are still so many gaps that the practical problem of separating exactly successive species and precisely common ancestral populations does not arise as often as Darwin seems to have expected. For a good recent review of this subject, one of several, see Imbrie (1957).

PHYLOGENETIC CLASSIFICATION

What Darwin proposed was that classification should have a single theoretical basis: phylogeny or, in his own terms, propinquity of descent. The individual characteristics of organisms were no longer to be the *basis* for classification; they were to be *evidence* on which to base judgment as to physical, evolutionary affinities among organisms. The importance of morphological and related criteria was to be determined, first, by their reliability as indications of propinquity of descent and, second, by the hierarchical rank or the scope of the group that they characterize. Darwin recognized and discussed four kinds of evidence for bringing different organisms into one taxonomic group:

1. Characters in common, the old "type" interpreted as heritage from a common ancestor.
2. Chains of contemporaneous species (or genera, etc.), interpreted as diversification from a common ancestry without extinction of intermediate forms.
3. Lineation in time, the temporal succession of progressively modified forms interpreted as the actual record of descent.
4. Visible or immediately inferable community of genetic origin.

The last mentioned category, which we have not mentioned before, is the most obvious or indeed the only direct approach to classification by propinquity of descent. Of it Darwin says:

> With species in a state of nature, every naturalist has in fact brought descent into his classification; for he includes in his lowest grade, or that of a species, the two sexes; and how enormously these sometimes differ in the most important characters is known to every naturalist: scarcely a single fact can be predicted in common of the males and hermaphrodites of certain cirripedes, when adult, and yet no one dreams of separating them.

He then adds the cases of sequential larval stages, different from each other and from the adult, of "alternate generations," [24] of "monsters," of "varieties," [25] and of what we would now call polymorphism. It was then and is now truly a familiar fact that the differences among members of a single species are very frequently—perhaps in an absolute majority of instances—greater than those between some members of distinct species. Applied at this level strictly morphological classification leads to absurdities so manifest that here even the most rigid idealistic typologist or morphologist abandons the principle of characters in common and adopts that of descent. It is true that *direct* evidence of descent is rarely applicable outside of species and never at high levels in the hierarchy. On this point Darwin cogently proceeds:

> As descent has universally been used in classing together the individuals of the same species . . . and as it has been used in classing varieties which have undergone a certain, and sometimes a considerable amount of modification, may not this same element of descent have been unconsciously used in grouping species under genera, and genera under higher groups, though in these cases the modification has been greater in degree, and has taken a longer

[23] It should be mentioned that Darwin's typological solution was not really practical in any event. He himself noted that it did not necessarily permit us to "separate and define the groups to which such types belong"—but such separation and definition (in some terms, not necessarily those of characters in common) are essential in practical classification. It is thus fair to say that some paleontologists and others are on the wrong track when they advocate a return to typological or "purely morphological" classifications because of these particular difficulties in phylogenetic classification.

[24] Meaning alternation in animals, e.g., coelenterates. We may add the more widespread occurrence of so-called alternate generations in plants.

[25] At this point Darwin means a normal individual variant within a population. Elsewhere he often uses "variety" to mean a population which as a whole differs from other populations within a species. He never makes this distinction clear and seems, indeed, to be unaware of its importance. He also included the forms of polymorphic species under "varieties," although he here mentions them separately. In the sixth edition the example of polymorphism (in orchids) is omitted, and so is a really charming *reductio ad absurdum* in which Darwin discusses the classification of bears descended from a species of kangaroos and of a kangaroo born to a she-bear.

time to complete? I believe it has thus been unconsciously used. . . . We have no written pedigrees; we have to make out community of descent by resemblances of any kind.

And he then goes on to show, as we have already discussed above, how the various criteria of classification can be interpreted and used in this way.

The last sentence of the preceding quotation has a special bearing on the most important objection that has been raised against Darwinian or, more generally, evolutionary classification (e.g., by Blackwelder and Boyden, 1952). It is argued that because we do not (in most cases) have "written pedigrees" the goal of evolutionary classification to "express phylogenetic relationships" is chimerical and that phylogeny is quite untenable as a taxonomic principle.[26] It is quite true that current classifications (at least those covering groups of considerable magnitude) do not in a strict sense "express" phylogeny. The goal of achieving a reasonably secure written pedigree has been approached in some groups and will doubtless be achieved for many, but it probably is chimerical for the organic realm as a whole or even for a majority of organisms. The excessive optimism of some of Darwin's immediate followers, such as Haeckel (e.g., 1894–1896), did give some grounds for both theoretical and practical criticism of phylogenetic classification.[27] Even if we do have a good phylogeny for a group, literally *expressing* it in a written classification is not possible. The intricate details of branching, the varying lengths of myriad segments, the complex and shifting nature of the organic comparisons—these cannot possibly be accurately expressed in a classification. I doubt whether any taxonomist ever thought that they could be, although some may have used the word "express" carelessly. Darwin understood this matter perfectly well. He clarified the relationships between phylogeny and natural classification, which cannot represent or express phylogeny but must be based on it, by remarking on his theoretical diagram of phylogeny in Chapter IV (the only figure in the book):

> If a branching diagram had not been used, and only the names of the groups had been written in a linear series, it would have been still less possible to have given a natural arrangement; and it is notoriously not possible to represent in a series, on a flat surface, the affinities which we discover in nature among the beings of the same group.

Darwin made it clear that it is neither necessary nor to be expected that a concretely expressed phylogeny—"pedigree" in Darwin's terminology—will be at hand for a group that is nevertheless to be classified on the basis of phylogenetic affinities—"propinquity of descent." Quaint as the expression now sounds, it is unfortunate that we have replaced "propinquity of descent" by "phylogenetic relationships." Darwin's term may make it clearer that in practical classification one is, as a rule, concerned with degrees of relationship that result from phylogenetic events, and not necessarily with those events in themselves. It would be ideal if the "pedigrees" were known, but it is not absolutely necessary to know them in order to arrive at a fair judgment as to their results. In morphological terms, then, the main problem of evolutionary classification is to judge what resemblances are homologous, and hence bear on propinquity of descent, and what ones are homoplastic, and hence do not. Conversely, with differences the problem is to determine the extent to which they negate evidence for propinquity of descent, or to which they indicate distinctness of descent.

It is true that the complications in judging the significance of resemblances and differences may be very great. The complications are, however, decreased and not increased by the phylogenetic approach. The complications result from phylogeny, and a rational attack on them can hardly be made without taking that fact as basic. One complication treated by Darwin, which incidentally shows again that Darwinian, evolutionary classification does not even attempt to *express* phylogeny, is that equal degrees of resemblance do not necessarily indicate equal degrees of phylogenetic affinity. This is true, at least, if phylogenetic affinity is thought of in terms of generations or of time elapsed between successive groups or since the common ancestry of contemporaneous groups. It seems natural to represent a graphic phylogeny or written pedigree in those terms, but it is rarely practical to represent such degrees of affinity ac-

[26] Hand in hand with this argument go objections to the evolutionary understanding of homology and confusion as to classification of characters as against the use of characters as evidence for classification. Those points have already been considered at sufficient length.

[27] Haeckel's views were, nevertheless, neither so extreme nor so vulnerable as some critics have suggested. He seems to have understood the distinction between using morphology as the objective evidence for classification and using phylogeny as the logical basis for its interpretation. The fact that some of Haeckel's phylogenetic trees were based on insufficient evidence or faulty interpretation is entirely beside the point here.

curately in classification. Some lineages evolve more rapidly than others and some branches from a common ancestry diverge more rapidly than others. So in another sense the degree of affinity, even of genetic affinity, is less in some cases than in others even though the time or number of generations elapsed may be the same. This, too, was clear to Darwin:

> I believe that the *arrangement* of the groups within each class, in due subordination and relation to the other groups, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups, though allied in the same degree in blood [i.e., number of generations in genealogy] to their common progenitor, may differ greatly, being due to the different degrees of modification that they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders. . . . So that the amount or value [in taxonomy] of the differences between organic beings all related to each other in the same degree in blood has come to be widely different. Nevertheless the genealogical *arrangement* [grouping by propinquity of descent] remains strictly true, not only at the present time, but at each successive period of descent.

THE NEW SYSTEMATICS

In *The Origin of Species* Darwin did not propose any explicit changes in classifications then current. On the contrary, he took them as given and as embodying in a symbolic or formal system a large body of facts. He then demonstrated that these facts are all explained if they are viewed as the results of evolution.[28] The aptness and completeness of the explanation is in turn the strongest sort of evidence for the truth of evolution. Darwin was well aware that his views also provided a new taxonomic principle, that of propinquity of descent, but this had little immediate impact on the practice of classification. Even though they had no acceptable theoretical criterion for evaluating resemblances or characters in common, the nonevolutionary taxonomists had a fixed conviction that some are more important than others and that some are misleading and result in unnatural classification. Those taxonomists were frequently successful in making evaluations that are also valid to an evolutionist. That is surprising at first sight, but less so when one considers that evolution by its very nature must tend to produce fundamental relationships that may be quite recognizable even when their cause is unknown. When the relationships are not fairly obvious, pre-Darwinian classifiers were hardly more successful than would be expected by chance. For instance a majority of them recognized that whales are fundamentally similar to mammals but not that aardvarks are fundamentally dissimilar from edentates.

Since Darwin the form of classification remains little changed from the Linnaean hierarchy. Although hopelessly unsuitable for expressing phylogeny, the hierarchy is reasonably successful in reflecting propinquity of descent. It is, indeed, far from ideal, given the fact that the chain of being, or ladder of nature, which it *could* express, does not exist. Nevertheless, it works fairly well for evolutionary classification and no one has yet been able to devise a better, practical formal framework. Thus there was no revolution either in the form or content of classification when Darwin's revolutionary taxonomic principles were accepted. The form has been slowly and slightly modified only by the tendency to use a larger number of categories as the number of taxa (actual groups of organisms recognized in classification) has increased immoderately. The content of classification has changed profoundly, but also gradually. The great increase in number of taxa has resulted partly from discovery and partly from splitting or downgrading of categories. (Most of Linnaeus' genera are now families or still higher groups.) Application of the Darwinian criterion of propinquity of descent also eventually led to great changes in classification. These could not be achieved overnight or even overcentury, and the reworking of the system on this principle is still going on. Many more facts were—and are—needed, and the revision of classification would in any case have been a long task if only because the number of taxonomists has always been so small in proportion to the number of groups requiring revision.

[28] The nature of explanation in science has been much discussed lately. In biology explanation is generally of three kinds:

1. Historical or evolutionary, by the sequence of events and changes through time that have produced an observed result.
2. Adaptational or teleonomic (Pittendrigh, 1958), by the utility to a given organism or population of its observed structures, activities, and ecological relationships. (This is sometimes called "functional" but at the risk of confusion with the next category.)
3. Physiological or reductional, by the mechanical or chemical operation of the structural elements in organic systems.

Explanation in *The Origin of Species* is almost exclusively historical even when it is concerned with functional or physiological characteristics.

So far we have spoken of the carrying out of a taxonomic task foreseen and defined by Darwin, although he inevitably underestimated its magnitude. There is, however, a new systematics which goes beyond Darwin in several respects. In part, to be sure, "the new systematics" is only an expression to unite fields of study most of which were already separately established in Darwin's day. It brings together all aspects of science concerned with organic diversity and hence parts but not the whole of morphology, physiology, cytology, biogeography, ecology, genetics, psychology, stratigraphy, etc., along with its central discipline of taxonomy. This new designation of a common area among different sciences is not mere form or artifice. It has helped to rejuvenate taxonomy by broadening its base.

For Darwin, most taxonomists before him, and some since him, the data of taxonomy were almost exclusively morphological.[29] Darwin even argued against the previous admission of physiological (including behavioral) data, on the then sound grounds that previous use of such data, subject as they are to converge, had been misleading as to propinquity of descent. It is still true that most taxonomic data are morphological, but only as a matter of necessity and not of principle. Physiology and behavior are not necessarily misleading as to phylogenetic relationships and may, on the contrary, be highly enlightening when properly evaluated. (See, e.g., Mayr, 1958.) Ecology, genetics, biogeography, biostratigraphy—not to mention such developments as biochemistry within physiology or cytology within anatomy—these and indeed *all* observations on organisms also yield evidence on phylogeny or propinquity of descent. All are therefore now considered pertinent for classification and all are used to the extent that observations on them are practicable.

That is still carrying out Darwin's program by other or extended means. The new systematics also involves a more definite and essential, although perhaps rather subtle, break with Darwin and his more immediate followers. There has finally been a complete abandonment of typology and the substitution of population concepts, with the related more direct involvement of genetics (especially as population genetics) in taxonomy.[30] It has been noted above that Darwin's thinking was still essentially typological, even though he supplemented typology by other concepts and even though he discarded previous theoretical interpretations of typology, such as they were. He still thought of taxonomic groups in terms of a pattern of characters in common, explicitly called a "type" in Darwin's own terminology, a fixed and static representation of the group at any given horizon even though Darwin of course saw the type changed as the group evolved. Darwin also of course observed that variation occurs within all natural populations—that is, indeed, the *sine qua non* of evolution by natural selection. But a "variety" also was or had a "type," whether it was an individual variant within a population or a variant population within a species, and was defined by divergence from the specific "type." Moreover, the distinction between individual, local (nonisolated) population, and genetically isolated species is never quite clear in *The Origin of Species*.

In the new systematics, a taxonomic group (taxon) is a population and is defined as such. It cannot, by its nature, have a type, either as a concrete individual or as an abstract plan.[31] It embraces *all* individuals of the population, and furthermore the individuals are continuously changing. It has a pattern, but the pattern is one of development and variation, for only such a pattern can in fact include and characterize the totality of a population. And all taxa are genetical units, *defined* by their reproductive relationships although they are usually *recognized* by physical characteristics. That distinction, perhaps esoteric at first sight, may be clarified by the analogy of identical twins: we recognize their relationship by the fact that they look alike, but they are not twins because of their resemblance, which is a result of the reproductive relationship that defines the twinship. The primarily genetical definition of taxa is a logical step from Darwin's explanation of the morphological characteristics of taxa, but its full genetical understanding was beyond possibility for anyone in Darwin's time.[32]

[29] Darwin did admit the possible pertinence of biogeography, but briefly and with evident misgivings.

[30] There are of course still typological and non- or even anti-genetical taxonomists, but they are not concerned with "the new systematics" and they represent, in my opinion, the past and not the future of taxonomy.

[31] Types are still used in nomenclature, where they are a completely arbitrary, legalistic device and have nothing whatever to do with the recognition or definition of natural taxa. It is extremely unfortunate that perpetuation of the term in this quite different sense permits and even encourages confusion.

[32] This would still have been true if Darwin or other pre-1900 evolutionists had paid attention to Mendel's experiments. Mendel's work had no immediate bearing on population systematics, and Mendel himself seems to

Thus in the history of taxonomy, the following approximate sequence of steps has occurred:

Classification: (*a*) by gross resemblance, intuitively evaluated.
(*b*) by typology (abstraction of characters in common) or alternatively by lineation in the "chain of being," in either case on transcendental or creationist principles.
(*c*) by typology, primarily, and lineation, in a supplementary way, both interpreted phylogenetically.
(*d*) by populations defined by genetical relationships.

Each step has developed from those before it. Explicitly, modern taxonomy (*d*) is firmly based on (*c*), which was Darwin's taxonomic system.[33]

SUMMARY

Descriptive comparative anatomy developed during the three centuries preceding publication of *The Origin of Species*. It rose to the level of a theoretical science with the gradual recognition of essential similarities, eventually called homologies, among otherwise diverse groups of organisms. Pre-Darwinian attempts to explain homology generally involved a pattern, type, or archetype which was either itself left unexplained, equated with a Platonic "idea," or considered a plan followed by the Creator. Darwin explained homology by inheritance of the homologous characters from a common ancestry. This further supplied hitherto lacking scientific definition and criteria for homology, giving the term the evolutionary significance now generally (although not quite universally) accepted. Darwin further discussed, although at first in a somewhat inadequate way, the existence of nonhomologous resemblances, a phenomenon for which the (post-Darwinian) term homoplasy is now available. He distinguished resemblances caused by adaptive convergence, now generally called analogies, and those caused by mimicry.

Pre-Darwinian classification developed two principles, which were usually poorly distinguished in theory and often mingled in practice. One involved the *scala naturae* or "chain of being" which supposed all organisms to form a series from simple to complex, imperfect to perfect. The other principle was akin to idealistic morphology and recognized an arrangement of groups within groups, defined by characters in common and corresponding with idealistic patterns or types. Neither system was explanatory and although both were attempts to achieve a "natural" arrangement, their theoretical basis was transcendental and not natural. Darwin accepted the typological, group-within-group concept and showed that when it is valid it is truly natural, a reflection of different degrees of propinquity of descent within the various groups. There is no single chain of being, but there are many different chains, which if natural reflect stages in evolutionary progressions. Darwin recognized that formal, hierarchical classification cannot express phylogeny but can and, if it is to be truly natural, must be based on propinquity of descent. With some minority dissent, those principles are accepted in modern, evolutionary taxonomy. Apart from the complications of increasing knowledge and more detailed analysis, systematics has developed beyond Darwin principally in completely replacing typological by population concepts and in more explicitly and consistently recognizing genetical relationships as the sole ultimate theoretical basis of taxonomy.

ADDENDA

1. Since submitting this paper I have noted that although Ray did, indeed, on occasion place the whales among the fishes, he knew better. In fact he explicitly condemned that arrangement and followed it only in deference to the opinions of other naturalists. The fact that this *was* the general opinion of naturalists as late as 1700 illustrates my point even better than ascription of the view to Ray himself.

2. In a recent paper Cain (1958; reference inserted in the list of references) has pointed out that the term "natural" may have been used by Linnaeus and others of his period in a highly technical sense derived from Aristotelian and Thomist philosophy. "It is likely that for [Linnaeus] a 'natural' system was one that showed the

have had no inkling of its possible importance for taxonomy. Indeed Mendelian genetics, strictly speaking, is *typological*.

[33] Citation of thousands of studies of the new systematics and of evolutionary, genetical classification would be useful but is not practicable here. The following small sampling may serve to clarify and support the present brief statement, and to lead into the literature: Brown and Danielli, 1953; Dobzhansky, 1951; J. Huxley, 1940; Mayr, 1957; Mayr, Linsley and Usinger, 1953; Simpson, 1945; Stebbins, 1950.

natures of things, and that natures meant in practice essences." (An essence is "the true entity of a thing considered in the order of existence" according to Aquinas.) That is, however, a *non-natural* (metaphysical, supra- if not supernatural) concept in the now usual vernacular and biological sense of "natural" and "nonnatural." This helps to clear up the doubts, inherent in my preceding discussion, as to just what "natural classification" could mean to a pre-evolutionist. It still more strongly emphasizes the change from Linnaean to Darwinian classification. It also, in my personal opinion, illustrates how inappropriate Aristotelian and Thomist principles are for natural classification in the now current sense of the words.

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DARWIN AND ZOOGEOGRAPHY

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(*Commemoration of the Centennial of the Publication of* The Origin of Species *by Charles Darwin, Annual Meeting of the American Philosophical Society, April, 1959*)

ZOOGEOGRAPHY is the study of the geographical distribution of animals, the study of where different animals are on the earth, and how and why they got there, and what their presence in particular places means.

I want to begin by asking what zoogeography—animal distribution—did for Darwin. The answer is that it showed him evolution. What he saw of the distribution of animals in South America and on the Galapagos Islands really was the thing that set Darwin off on the track of evolution, although he had other hints of it too. What he saw on the Galapagos was most important of all. He had already been struck by the basic similarity of different species of plants and animals in different places and different habitats in South America and by the similarity of some of the fossils he had found to the living animals—it was the distribution as well as the nature of the fossils that impressed him, the fact that some of the most curious ones were on the same continent as the living animals they resembled. And on the Galapagos he finally saw how evolution makes different species in different squares of a geographical chess board—I shall come back to this later (p. 316).

What Darwin saw in South America and on the Galapagos was something fundamental in the pattern of plant and animal distribution. There are, as Darwin realized, two possibilities. If species were individually created, each made to fit a particular environment and set down separately there, the different species created and designed for, say, the desert environment ought to be much the same in all deserts, even in the most widely separated parts of the world. But if species were products of evolution, of descent from long lines of ancestors, they could only occur where their ancestors occurred or in places they could reach from there, and species in, say again deserts, would be likely to be very different in different deserts, derived from different ancestors. In the first case, similar species should be scattered all over the world, regardless of distance and barriers; in the second case, similar species should be confined to the same or connected geographical areas. It is this second pattern, the result of the fact that where species now occur depends on where their ancestors occurred, that is fundamental in plant and animal distribution and that Darwin saw, unmistakably, in South America and the Galapagos. What this pattern really showed Darwin was that species have ancestors. This fact is commonplace now but it was cataclysmic then.

Darwin's own examples of the fundamental fact that the distribution of plants and animals depends on the distribution of their ancestors are still good examples. He says, in *The Origin of Species* (2: 295),[1]

> . . . if we compare large tracts of land in Australia, South Africa, and western South America, between latitudes 25° and 35°, we shall find parts extremely similar in all their conditions, yet it would not be possible to point out three faunas and floras more utterly dissimilar . . . [but if we] compare the productions [plants and animals] of South America south of lat. 35° with those north of 25°, which consequently inhabit a considerably different climate [in the first case open pampas in the south temperate zone and in the second tropical forest], . . . they will be found incomparably more closely related to each other than they are to the productions of Australia or Africa under nearly the same climate.

Darwin saw that this must be the result of evolution of the pampas and rain forest species from common, American ancestors. And later in the same book (2: 337) he says,

> The most striking and important fact for us in regard to the inhabitants of islands is their affinity to those of the nearest mainland, without being actually the same species. Numerous instances could be given of this fact. I will give only one, that of the Galapagos Archipelago, . . . between 500 and 600 miles from the shores of South America. Here almost every

[1] Numbers in parentheses indicate references at end of article.

product of the land and water bears the unmistakable stamp of the American continent . . . . Why should this be so? Why should the species which are supposed to have been created in the Galapagos Archipelago, and nowhere else, bear so plain a stamp of affinity to those created in America?

Of course the answer must be, as Darwin saw, that the Galapagos species have not been separately created but have been formed, by evolution, from American ancestors.

The sort of geographic pattern that evolution makes and that Darwin saw can be diagrammed by means of phylogenetic trees. Two such trees are shown in figure 1, as drawn by Darwin for *The Origin of Species* (2: 90–91). A "tree" like this is really a simple plan of the evolution of a group of plants and animals. The base represents a common ancestor. The main trunks represent different groups of plants or animals that have evolved from that ancestor. And the branches represent smaller groups that have evolved from the main ones. For example a diagram something like this (fig. 1, left) might show the evolution of the higher primates. If this diagram of Darwin did represent the evolution of the higher primates (which it is not designed to do), then *A* might be a monkey-like common ancestor, *m* might be the line of evolution of monkeys, *a* might be the line of evolution of the great apes, and *f* might be the line of evolution of man.

An evolutionary tree like this can be laid on a map to show how evolving animals have moved over the earth (fig. 2). Suppose the common ancestor (*B*) of a group of animals lived in tropical Asia, and suppose three different lines evolved from it and, as they evolved, moved in three different directions, *b* to Africa, *c* across the islands to Australia, and *d* through North and South America. And suppose each line ramified in its own part of the world, by evolution. If the results were plotted on a map of the world, we should get a picture of evolution and movement something like that in figure 2. The central part of this diagram is mine, but the branches are Darwin's, partly reversed and with a few superfluous twigs cut off. If the branches do not fit the land exactly, that is because Darwin did not plan them to fit any particular piece of land.

I do not know whether Darwin thought of the tree simile while he was on the *Beagle*, but he did think of it later. He put it in a wonderful, Victorian sentence at the end of Chapter 4 of the *Origin* (2: 113). He says,

> As buds give rise by growth to fresh buds, and these, if vigorous, branch out and overtop on all sides many a feebler branch, so by generation [he meant by evolution] I believe it has been with the great Tree of Life, which fills with its dead and broken branches the crust of the earth [the dead and broken branches are fossils of extinct plants and animals], and covers the surface with its everbranching and beautiful ramifications.

Whether or not Darwin thought of the tree while he was on the *Beagle*, he saw parts of it then. He saw that American plants and animals, including the fossils he found, belonged to American branches (*d* of fig. 2) of the tree, not to African or Australian branches. And he saw on the Galapagos Islands how a few small branches, always from America (from *d*) had reached the archipelago and split into twigs there, the twigs being slightly different species on different islands. All this, the main pattern as well as the details of animal distribution, showed Darwin, as I have said, that species have ancestors and must have been produced by evolution.

A digression or two are in order now.

I have said that it was zoogeography—animal distribution—that set Darwin off on the track of

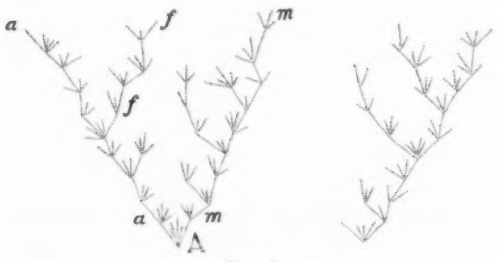

FIG. 1.

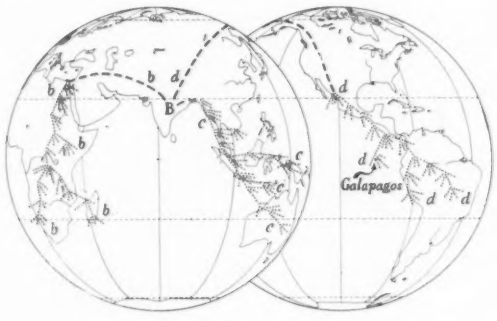

FIG. 2.

evolution, but you may have heard that it was reading Malthus that set him off. Malthus was important, but he came second. There were two steps in the development of Darwin's theory: first realization of the fact of evolution, then explanation of it. What he saw of animal distribution (and, eventually, much other evidence) convinced Darwin that evolution was a fact. Malthus suggested the explanation. Malthus' essay (6) on human populations (he said populations increase indefinitely until surpluses are cut back by famine or other disasters) suggested to Darwin that all plants and animals produce too many offspring, that only part can survive, and that competition and survival of the best offspring—natural selection, survival of the fittest—was the mechanism of evolution.

Zoogeography — animal distribution — showed Wallace evolution too. Wallace too saw, from the pattern and details of animal distribution not in South America but in the Malay Archipelago, that species have ancestors and that evolution must be a fact. Then he too happened to read Malthus, and he too thought of natural selection. It is outside my subject to repeat how Wallace's duplication of Darwin's theory forced Darwin at last, after more than twenty years of thinking and accumulating facts, to publish his theory. But I want to emphasize that Darwin and Wallace not only reached the same conclusions but reached them in the same way. Both men first deduced the fact of evolution primarily from what they saw of animal distribution, and both then drew the same explanation from the same source, from Malthus. This surely shows something about the times they lived in. It shows that the time had come for the discovery of evolution and the beginning of explanation of it.

For example, both Darwin and Wallace were greatly indebted to the men who had gradually built up classifications of plants and animals to the point where fundamental similarities, what we now call relationships, were becoming increasingly visible. Darwin saw what he called the "unmistakable stamp" of the American continent on the animals of the Galapagos. Did it occur to him that generations of naturalists had had to collect animals and plants all over America, and slowly and laboriously classify them in an increasingly natural way, before the "American stamp" could be seen at all, and that the plants and animals of the whole world had to be reasonably well known before it could be seen that the stamp was really peculiar to America? The tenth edition of Linnaeus' *Systema Naturae*, on which we base our system of naming animals, was published a century —actually 101 years—before *The Origin of Species*. Linnaeus' work was a product of his times —the time had come for a uniform method of naming and classifying animals—but another century of collecting more animals and improving classifications was necessary before the times were ready for Darwin. Darwin's debt to the men who did this work can hardly be overestimated. He might (but I do not think he would) have postulated evolution without them, as the Greeks did, but, without the good start toward a natural classification of plants and animals and without the fairly detailed knowledge of plant and animal distribution that his predecessors gave him, he could hardly have proved it.

But to come back, this is what zoogeography—animal distribution—did for Darwin: it showed him, compelled him to see, that evolution was a fact. This was the initial fact from which all Darwin's ideas stemmed.

What did Darwin do for zoogeography? He did almost as much as zoogeography did for him. Acceptance of Darwin's evolution made it possible at last really to begin to understand animal distribution. Right up to the time of publication of *The Origin of Species*, in 1859, zoogeographers were arguing about centers of creation, not whether there were such centers, but how many there were and where they were, and whether identical animals were created at more than one place. For example Sclater (9) read a paper to the Linnean Society in 1857 and published it in 1858 in which he said that, if he could show the existence of separate centers of creation in different parts of the world, he could avoid

> the awkward necessity of supposing the introduction of the red man into America by Bering's Straits, and of colonizing Polynesia by stray pairs of Malays floating over the water like cocoa-nuts, and all similar hypotheses.

Darwin stopped this kind of thing. He showed that evolution of animals, and movement of the evolving animals over the world, could explain the main facts of animal distribution, and he supposed the details would fall into place later, although he did not pretend to explain all the details himself. Most of the details have fallen into place. We know now that the red man did reach America across Bering Strait, when there was a

land connection there, and that the Polynesians did float over the water, not exactly in pairs like coconuts, but in canoes.

Darwin did more for zoogeography than just to present an evolutionary theory that zoogeographers could use, although that was epochal. He was a zoogeographer himself. He contributed something to what was known of the facts of plant and animal distribution, and he contributed more to zoogeographical theory, especially in his two chapters on geographical distribution in *The Origin of Species* (2: chapters XI, XII).

Zoogeography, which is itself a subdivision of biology, can be analyzed and subdivided in turn. I am going to subdivide it, partly to show what zoogeographers are doing and trying to do, and partly to clarify Darwin's place in zoogeography.

Logically and historically the first subdivision of zoogeography is *descriptive zoogeography*. Its main purpose is simply to describe the details and patterns of animal distribution. Wallace was the great descriptive zoogeographer. His kind of zoogeography is sometimes called "static zoogeography," but it is a mistake to slight it. Other kinds of zoogeography depend on it. And descriptive zoogeographers see much more than the static patterns. Remember that Wallace discovered evolution too.

Ecological zoogeography treats animal distribution in relation to the environment. Descriptive zoogeographers do not ignore the environment; they understand its importance; but they usually consider it in a rather general way, in terms of climatic zones and broad areas of forests and deserts rather than in terms of microclimates. Ecological zoogeographers divide the environment into factors which they try to measure and assess exactly, usually in rather small areas. This is important, but it is ecology more than zoogeography. So far as it is zoogeographical, ecological zoogeography is essentially an extension of descriptive zoogeography to the local-habitat level. It describes, among other things, the limits that the environment sets to the distributions of particular animals at particular places at particular times.

The third subdivision of zoogeography is usually called historical, but I prefer to call it *evolutionary zoogeography*. I invented this term, then found that it had already been used at least once by Simpson. It is concerned with, first, the evolution of geographical patterns by movement of animals, by spreading, shifting, and extinction of populations, and, second, the relation of organic evolution to the geographical movements. These two kinds of evolution are different but interdependent.

These three subdivisions of zoogeography can perhaps be made clearer by an analogy. Compare a group of evolving, dispersing animals to a motor car. Descriptive zoogeography is concerned with the shape of the car and where it is at any particular time. Ecological zoogeography is concerned with steering and braking mechanisms, which can turn the car in certain directions and stop it at certain places, but do not propel it. And evolutionary zoogeography is concerned with the motor, with how and why the whole thing moves. This analogy is crude and oversimplified, but I think it is true as far as it goes.

It is worth while to illustrate these subdivisions by an actual case. If we want to understand the distribution of animals in the arctic, we begin by mapping the ranges of arctic species. This is descriptive zoogeography; it is indispensable at the beginning. Then we analyze the life histories and adaptations and tolerances of the animals in relation to distribution, noting especially the limits set by cold and by the shortness of arctic summers. This is ecological zoogeography; it too is indispensable; we could not possibly understand the distribution of animals in the arctic without it. But when it is done, something unexpected and important is still unexplained. Suppose we have been working with amphibians—salamanders and frogs—then we will have discovered that the northernmost amphibians are not the ones that seem to be most specialized to live in cold places. Most salamanders live in cool or cold places, and they have probably done so for a very long time; most of them cannot now live anywhere else. They are what ecologists call cold-adapted, thoroughly fitted to live in (and only in) cold places. Salamanders are abundant in cold north-temperate areas. But as we go farther north into the real arctic all salamanders disappear and the only amphibian left is a rather ordinary frog. This is the unexpected and important fact. The frog is adapted to the arctic, of course. Its legs are shortened, which probably reduces the chance of freezing, and it passes through the tadpole stage very rapidly, so that it can complete this stage of its life history during the short arctic summer. But it is still a rather ordinary frog, not primarily cold-adapted. What is the real reason that it is widely distributed north of the northern limit of salamanders? To answer this question we have to

turn to evolutionary zoogeography. Then we find that the arctic frog belongs to a genus, *Rana*, that apparently arose in the Old-World tropics and has spread over most of the world from there, and that has been (among amphibians) uniquely successful in many places and many habitats, from rain forests to deserts, and from the tropics through the north-temperate zone to the arctic. The arctic frog has apparently inherited from its Old-World-tropical ancestors general qualities that (with appropriate but rather superficial special adaptations) account for its success in the arctic as well as in other climates, although just what the qualities are is still unknown. This case suggests that even local ecological situations cannot be understood without taking evolution and the whole world into account.

Darwin's contributions to descriptive zoogeography were not very important. He got more from it—his first clear sight of evolution—than he gave it. I shall let others judge him as an ecological zoogeographer. It is as an evolutionary zoogeographer that he was and is pre-eminent.

First of all, Darwin never forgot that he was dealing with living things. Zoogeographers are constantly concerned with ranges. A range is a geographical area occupied by a kind of animal or a group of animals. In thinking about ranges some zoogeographers think too much about the geographical patterns and too little about the living animals that make them. These zoogeographers block out ranges on maps and treat them as if they were solid, permanent shapes. For example, certain African beetles have relatives in Brazil, and some zoogeographers think that the shapes of their ranges have not changed for a hundred million years, since a time when (they think) Africa and Brazil were joined together. But ranges are not like that. They are areas inhabited by populations of living animals, which die and are reborn every generation, which as populations are continually spreading and contracting, and which can and often do move rapidly over the earth. Ranges are like shadows cast on the earth by living, moving animals. We know from the fossil record that the ranges of many animals have in fact been no more stable during geological time than cloud shadows during a windy afternoon. Darwin did not use this simile, but as a zoogeographer he never forgot that he was dealing with living, moving animals.

Second, as a zoogeographer Darwin understood the fundamental importance of evolution in animal distribution. He understood that evolution not only explains the details of distribution that he saw in South America and the Galapagos but also explains the underlying, world-wide patterns and processes. He saw, for example (*2*: 95–97) that there must be a relation between evolution and extinction, that, as new kinds of animals evolve, multiply, and spread, older competing animals must become rare or localized and finally extinct. He saw that extinction must be a very common thing, and that it explains discontinuities. It explains, for example (but this is not Darwin's example), those beetles in Africa and Brazil, without changing the position of continents. The beetles were probably once widely distributed over the world but have become extinct everywhere except in Africa and Brazil. And Darwin went farther than this. Because he saw the relation of evolution to extinction, he was able to see also how successive "dominant forms of life" (*2*: 292) rise and spread over the world, each dominant group competing with, destroying, and replacing older groups, then differentiating in different places until overwhelmed by the rise and spread of the next dominant group. All this appears, somewhat disjointedly, in the summary of chapter X and the first pages of chapter XI and elsewhere in *The Origin of Species*. We know now that this process of evolution, spread, and replacement of successive dominant groups is the main process (infinitely more complex in detail than my description of it) that makes the main patterns in animal distribution.

Darwin read the past with extraordinarily good judgment. He understood how changes of climate affected northern floras and faunas before and during the ice age. This is not only discussed in the *Origin* (*2*: 311 ff) but also summarized in a letter to Asa Gray in 1858, as follows (*3*: 218):

> In the . . . Pliocene age (a little *before* the Glacial epoch) the temperature was higher [than now]. . . . At this period when all animals and plants ranged . . . nearer the poles, I believe the northern part of Siberia and of North America, being almost *continuous*, were peopled (it is quite possible, considering the shallow water, that Behring Straits were united, perhaps a little southward) by a nearly uniform fauna and flora. . . . The climate then became gradually colder till it became what it is now; and then the temperate parts of Europe and America would be separated, as far as migration is concerned, just as they now are. Then came on the Glacial period, driving far south all living things; middle or even southern Europe [and parts of temperate Asia and

North America] . . . [were then] peopled with Arctic productions; as the warmth returned, the Arctic productions slowly crawled up the mountains as they became denuded of snow; and we now see on their summits the remnants of a once continuous [arctic] flora and fauna.

All this is essentially correct. It correctly explains why many temperate Eurasian and North American plants and animals are now related but distinct species, and why we find arctic plants and insects on mountain tops in the temperate zone, on Mount Washington for example. Credit for this explanation properly goes to Edward Forbes, who published it first, although the explanation occurred to Darwin four years earlier (3: 218).

Darwin also suggested (2: 324) that, in "a former and warmer period" before the ice age, Antarctica was free of ice and supported a peculiar flora and fauna, parts of which reached southern South America, Australia, and New Zealand "by occasional means of transport" across the sea, using now-sunken islands as stepping stones. This is still as good a theory as any to account for the fact (it is a fact) that some plants and insects of the southern tip of South America, southern Australia, and New Zealand are closely interrelated.

In one way Darwin was far ahead of Forbes, in understanding if not in time of publication. Forbes plunged for great land bridges across the deep oceans. But Darwin held back, looked at the evidence, and carefully and correctly split the difference between the two possible extremes. He says (2: 303–304),

> Changes of level in the land must also have been highly influential: a narrow isthmus now separates two marine faunas; submerge it, or let it formerly have been submerged, and the two faunas will now blend or may formerly have blended: where the sea now extends, land may at a former period have connected islands or possibly even continents together, and thus have allowed terrestrial productions [plants and animals] to pass from one to the other . . . but to the best of my judgment we are not authorized in admitting . . . enormous geographical changes within the period of existing species. It seems to me that we have abundant evidence of great oscillations of level in our continents, but not of such vast changes in their position and extension as to have united them within the recent period to each other and to the several intervening oceanic islands. . . . Several facts in distribution—such as the great difference in the marine faunas on the opposite sides of almost every continent, the close relation of the tertiary inhabitants of several lands and even seas to their present inhabitants, a certain degree of relation . . . between the distribution of mammals and the depth of the sea—these and other such facts seem to me opposed to the admission of such prodigious geographical revolutions within the recent period as are necessitated on the view advanced by Forbes. . . . The nature and relative proportions of the inhabitants of oceanic islands likewise seem to me opposed to the belief of their former continuity with the continents. Nor does their almost universally volcanic composition favour the admission that they are the wrecks of sunken continents; if they had originally existed as mountain ranges on land, some at least of the islands would have been formed, like other mountain-summits, of granite, metamorphic schists, old fossiliferous or other such rocks, instead of consisting of mere piles of volcanic matter.

Besides this (and more) in the *Origin*, Darwin in 1856 (3: 160–164) wrote a "tremendous" letter on the subject to Lyell. I can quote only parts of it. He says,

> In all North and South and Central America, we have both recent and miocene (or eocene) shells, quite distinct on the opposite sides, and hence I cannot doubt that *fundamentally* America has held its place since at least the miocene period.

and he gives other evidence from the distribution of living and fossil animals to show that Africa, India, and Australia have stood fundamentally as they now are "within the period of living organisms," by which he evidently means as far back as he can see by the evidence of the distribution of living organisms and their direct ancestors. He adds to this some items of geological evidence, especially the nature of oceanic islands (see preceding quotation), and says he is inclined to believe "that continents as continents, and oceans as oceans, are of immense antiquity," and in the *Origin* (2: 291) he says

> . . . as far as we can see, where our oceans now extend they have for an enormous period extended, and where our oscillating continents now stand they have stood ever since the Silurian epoch; but long before that period the world may have presented a wholly different aspect; . . .

Fifty-six years after the publication of *The Origin of Species*, W. D. Matthew (7) again reviewed the evidence—much more evidence than Darwin had, especially the evidence of a better known fossil record—and again decided that, although there must have been innumerable local changes, as far as he could see the distribution of

animals allowed no great changes in the position and connections of the continents. It should not detract from Matthew's work, which was a very important contribution to zoogeography, to ask how far Darwin anticipated it. In this particular matter Darwin fell short of Matthew in two ways, I think.

First, Darwin, who was writing on evolution and not on zoogeography, simply summarized his evidence; he did not organize it or present it in detail. For example in a passage quoted above he refers to "the nature and relative proportions of the inhabitants of oceanic islands" as arguing against land bridges. We have to turn elsewhere in the *Origin* (2: 330–337) to find that he meant that oceanic islands have only a limited variety of plants and animals, of kinds that he thought might have crossed water (he experimented with seeds to see how long different ones would float and live in salt water), and that there are proportionately few or no amphibians and land mammals (except bats) on such islands. Darwin thought that amphibians and flightless land mammals could not cross salt water at all. He was wrong about that; their distributions show that they do get across narrow salt-water barriers. But he was right that they form a relatively small proportion of the faunas of remote islands, and that their fewness is evidence against land bridges. Nevertheless, he did not present nearly as much evidence in as much detail as Matthew did.

The other way in which Darwin (inevitably) fell short of Matthew was in his understanding of time. Darwin does occasionally refer to "miocene (or eocene)" and "tertiary" situations, but his datings are usually imprecise until he comes to events immediately before and during the ice age. Matthew saw the past more clearly, in much more detail, and much farther back than Darwin did.

I think all this can fairly be summarized by saying that Darwin considered the evidence he had and decided that *as far back as he could see* the main pattern of land had been the same as now, although many details had changed. Fifty-six years later Matthew, with much more evidence, reached the same conclusion, but saw farther back and in much more detail than Darwin could. And now, with still more evidence, we can see still farther back and in still more detail than Matthew could, but the conclusion is still the same. As far back as we can see, the distribution of animals and other evidence suggest a main pattern of land like the present one, in spite of all the details that have changed.

Both Darwin and Matthew partly detected and partly deduced that evolving plants and animals move over the earth in definite directions. Darwin (2: 322–323) drew his evidence partly from what botanists told him of the directions of "migrations" of plants and from the directions of dispersal of weeds within historic times. His conclusions were that plants "have apparently migrated from the north to the south [more] than in a reversed direction," and that the "productions" both of isolated tropical mountains and of islands have everywhere "yielded to continental forms." His explanation (2: 322) is:

> I suspect that this preponderant migration from north to south is due to the greater extent of land in the north, and to the northern forms having existed in their own homes in greater numbers, and having consequently been advanced through natural selection and competition to a higher stage of perfection or dominating power than the southern forms,

and he refers (2: 322) to ". . . the more dominant forms, generated in the larger areas and more efficient workshops of the north," and (2: 324) to "The living waters . . . [that] have flowed with greater force from the north so as to have freely inundated the south."

Matthew, fifty-six years later, in 1915 (7), drawing his evidence from the distribution and fossil record of vertebrates, detected a general tendency for dominant groups to evolve in the north and move southward, but he suggested an explanation based primarily on climate rather than area. His thesis on this point (7: 3) was:

> Secular climatic change [occurring or at least beginning north of the tropics] has been an important factor in the evolution of land vertebrates and the principal known cause of their present distribution.

Matthew's work, as I have said, was a very important contribution to zoogeography. It came at a time when many zoogeographers, for example Scharff in 1912 (8) and Gadow in 1913 (5), seemed to have lost their power of critical judgment and were moving continents and building land bridges with little regard for zoogeographical principles or evidence. The evidence that Matthew presented and the way he presented it helped to counteract this; and Matthew's conclusions about the stability of continents (as far back as can be seen) and the history of islands were correct. In discussing directional movements Darwin gen-

eralized from a small amount of evidence drawn mainly from living plants and Matthew presented and analyzed much more detailed evidence drawn from fossil as well as living vertebrate animals, but the two men were dealing with different aspects of the same thing, the pattern that evolving organisms make as they move over the earth. Neither saw quite the whole pattern; Darwin saw it only in a very general way; Matthew saw some parts of it in much more detail than Darwin did; but I think it was Darwin rather than Matthew who had the right explanation. It seems to be primarily area—the relative sizes of land masses—as Darwin thought, and not variable northern climate as Matthew thought, that determines the place of origin and directions of dispersal of dominant organisms.

One of the things that evolutionary zoogeographers are trying to do now is to find just where dominant animals do evolve and in what directions they move. There are several ways of getting at this. One way is to try to trace the movements of single groups through their fossil records. This was Matthew's method, and it is the best method, when the fossil record is good enough. In a really good fossil record the earliest, most primitive fossils of a group will be at the place of origin, and later and more derivative fossils will clearly show directions of movement. Unfortunately, few fossil records are this good, and poor records may be very misleading.

Another way of detecting directions of movement is to try to find how animals have moved at certain critical places. Simpson (11) has done this by comparing successive fossil mammal faunas of Eurasia and North America; occurrence of particular animals first on one of these land masses and later on the other is clear evidence of direction of movement. The results are almost as if Simpson had had an automatic traffic counter at Bering Strait for the last 50 million years or so. He found that, although there has been much movement in both directions, there has apparently always been more movement (of mammals) from Asia to North America than the reverse. Simpson (10) has also analyzed the exchange of mammals between North and South America since a land bridge was formed between these continents perhaps two or three million years ago, after a long period of separation. He found that many mammals moved in both directions across the new bridge, but most of the South American ones that reached North America died out there (the opossum and porcupine are exceptions) while many North American mammals survived in South America, so that the exchange ended as a great movement from North to South America.

We now have many other clues to places of origin and directions of movement of animals, but I cannot take space to discuss them. We know now that dominant, successful animals do evolve more often in some places than in others and that they move or spread more often in some directions than in others. We know in other words that Darwin's "living waters" (above, p. 313), the invisible rivers that living things make as they evolve and flow over the earth, are not random but have a central pattern. There is a great reservoir of evolving, dominant animals in the main land area of the Old World, in Eurasia and Africa, and rivers flow out from there to Australia, and to North America and thence to South America, and to islands. We have ways of detecting these rivers that Darwin did not have. We know, from fossils, much more than he did about the geographical movements of different groups of animals. We have Simpson's measurements of flow of mammals across Bering Strait and from North to South America. We have much other evidence of directional movements from what we now know of the distributions and apparent histories of many different animals. With all the new evidence we are finally really beginning to see the main pattern, the system of invisible rivers, that evolving, moving animals make. And it is the same pattern that Darwin, with only scraps of evidence, saw at least vaguely a century ago! And the essential explanation is apparently what Darwin thought, that the most dominant animals evolve in the largest favorable areas because that is where the "most efficient workshops" are, with the largest populations, the most kinds of animals, and the most intense competition.

This river simile is too simple. The invisible rivers that evolving, moving animals make do not flow directly but are like tidal rivers that flow back and forth (but still have a net direction) and are so full of complex cross currents and whirlpools that the main flow is hard to see. The details of movement of land animals over the earth have been more complex than any conceivable kaleidoscope. But underneath the details there is the main pattern that Darwin saw and that we see more clearly now: evolution of successive dominant groups in the largest favorable areas and movement (spreading) to smaller areas, from the

great continents to smaller continents, and from all the continents to islands. Of course there are still details we do not know. We are not yet sure —authorities disagree—how climate modifies the main pattern in special cases. And there may still be zoogeographers who doubt even the existence of the main pattern.

I do not want to make Darwin's zoogeography sound better than it was. He did not write a separate treatise on the subject, but just discussed some aspects of it briefly in the *Origin*, which was intended as an "Abstract" on evolution. Some of his ideas, for example his concept of the relation of extinction to evolution and spread of new forms, were carefully worked out, but other ideas were scattered or fragmentary. What he says about movements from north to south and from continents to islands begins as a discussion only of certain plants and then is extended to the "productions" of continents and islands, and the actual evidence he cites is drawn mainly from directions of movement of organisms dispersed by man, and it is not clear how broad he intended his generalizations to be. However I think he said enough to show that he saw and understood all the fundamental concepts of evolutionary zoogeography. He saw how evolution produces a succession of dominant groups of animals, each of which spreads, overwhelms, and replaces earlier groups, then differentiates in different parts of the world until overwhelmed and replaced by the next group. He saw, if rather vaguely, that there is a main pattern of movement, that dominant groups tend to evolve on the big continents and spread to small continents and islands, and he suggested what now seems to be the explanation, that the great number of animals and intense competition in large areas cause the evolution of dominant animals. And besides this, he read the past correctly. He saw how events before and during the ice age had affected animal distribution and he saw that continents or parts of continents must have changed in height and shape, but he saw also that (as far back as he could see) the distribution of animals allowed no vast changes in the position or connections of the continents. Darwin was not guessing about these things. He presented evidence and reached correct conclusions. No one could have reached correct conclusions just by guessing. That he saw and understood *all* these things, which together are the whole heart of the subject, makes him pre-eminent in evolutionary zoogeography.

Perhaps pre-eminent is not the word. It implies recognition. Darwin's evolutionary-historical zoogeography is remarkable, but one of the most remarkable things about it is how little his zoogeography (as distinct from his evolution) influenced zoogeographers. It did not stop irresponsible zoogeography, but neither did Matthew, and neither has anyone else. The remarkable thing is that Darwin's zoogeography has had little influence on responsible zoogeographers. Matthew, for example, was surely a responsible zoogeographer but I do not think he ever mentioned Darwin in a zoogeographical context. Now zoogeographers are finally coming back to Darwin's ideas a hundred years after he published them in the *Origin*, but not because of his influence. It is because a mass of new evidence leads back to the same conclusions Darwin reached. Eminent or not, as an evolutionary zoogeographer he was extraordinarily, almost incredibly, right about a hundred years ahead of time.[2]

It seems to me that the discovery of evolution was comparatively easy. It was time to discover evolution (of course this does not explain why it was Darwin who made the discovery). What Darwin did zoogeographically was much more complex and difficult. In *The Origin of Species* he rather casually laid down all the main principles of the relation of evolution to animal distribution, and in the light of these principles and a little evidence he saw and understood not only the astonishing changes that have occurred in climate and in geographical details of the world but also that there is a limit to the changes, that animal distribution does not allow vast recent changes in position and connections of continents. Some other men saw some of this then and later, but I doubt that anyone but Darwin (and Wallace?) really saw it *all* until recently—now it is comparatively easy to see. I think that Darwin's zoogeography may be a better measure of his capacity than discovery of evolution is.

What qualities or experiences or habits did Darwin have that led him to discover evolution, anticipate modern zoogeographers, and do all the other things he did? Persons who know him better than I do, including Darwin himself, have

[2] What is now known and suspected of the relation of evolution to animal distribution is discussed in chapter 9 of my recent *Zoogeography* (12), and what animal distribution seems to tell of the past is discussed in chapter 10 of the same book. It would be interesting to compare Darwin's ideas with those of modern plant geographers, but I am not qualified to do it.

tried to answer this question without complete success. I can give only a partial answer.

Darwin's zoogeography and much of his other work depended on his discovery of evolution, and that was partly a matter of the time. It was his good luck to live when geologists discovered how the earth's surface has evolved, when botanists and zoologists had improved plant and animal classifications until real patterns of evolution and geographical distribution were becoming clear, and when biologists and other educated men were ready to take evolution seriously when it was properly presented to them. If Darwin had lived a generation earlier, he would have been too soon. If he had lived a generation later, evolution would already have been discovered.

But, granting that the time had come to discover evolution, why was Darwin the man who discovered it? The immediate (but not the final) answer is, because he went on the *Beagle*, and that was partly luck (3: 36). He was lucky to be asked; at least one other man had been asked first but had declined; and he almost lost the trip twice, once when his father refused permission but changed his mind, and once when Captain Fitzroy almost rejected him because of the shape of his nose—he thought Darwin's nose indicated lack of persistence! Darwin did discover evolution during the *Beagle* trip, and he would probably not have discovered it if he had stayed in England. The pattern of distribution of fossil and living animals that he saw in South America and on the Galapagos and that showed him evolution does not exist in England, or rather it is so confused that it is very hard to see. What struck him most of all was the occurrence, on the Galapagos, of slightly different species on the different islands. The surprise and importance of what he saw are expressed in his own words (1: 394),

> I never dreamed that islands, about fifty or sixty miles apart, and most of them in sight of each other, formed of precisely the same rocks, placed under a quite similar climate, rising to a nearly equal height, would be differently tenanted; but . . . I obtained sufficient materials to establish this most remarkable fact in the distribution of organic beings.

This pattern of differentiation that Darwin found on the Galapagos is produced by evolution in discontinuous areas where the environment has been reasonably stable. If the pattern ever existed in England, it was destroyed by the ice age. Suppose the Galapagos were a chess board. Evolution has placed pieces (evolving animals and plants) on it in a definite pattern so that an intelligent man (Darwin) can see what game is being played; but in England ice sheets and climatic changes have swept the pieces off the board and thrown them back again, almost at random so far as the original pattern is concerned. Wallace too had to leave England and go to the tropics to see the geographical pattern produced by evolution; Wallace's chess board was the islands of the East Indies.

That Darwin and Wallace both had to get out of the shadow of the ice age and go to the tropics to see evolution is more than an historical fact; it emphasizes something that is still true. It is still necessary to go to the tropics to see some aspects of evolution, and there are probably still important unknown things about evolution that can be discovered only in the tropics. At the very least one must know what has happened in the tropics in order to understand situations in other parts of the world, as that arctic frog shows. Several times in this paper I have mentioned ecology, always favorably, but always with an unspoken reservation. I have not so much a criticism as a question to ask. How many North American ecologists nowadays teach their students that they can learn all they need to know about animals and the environment by measuring details in small areas in the north temperate zone, and how many look to the tropics too? How many tell their students to *go* there? I know that some do, but how many do not?

Why (granting the element of luck) did Darwin go on the *Beagle*? The answer is because he was a naturalist. That answer takes us one step nearer to explaining Darwin, although it is still not a final explanation. A naturalist is "one versed in natural science; esp., a student of animals or plants," but that is not enough of a definition. A naturalist is interested in all the living things around him and the world they live in, and if he is a serious naturalist he wants to understand them as well as know their names. Darwin was that kind of naturalist. I think it has been said that he was the last naturalist, but he was not. My late director, Thomas Barbour, was a great naturalist, and so was my old professor William Morton Wheeler, whose interests ran from ants to philosophy. Oddly enough I have heard these two men, sitting together on the back steps of the Museum of Comparative Zoology (called informally the M. C. Z. or the

Agassiz Museum), say that they were the last naturalists, but they were not. I consider myself a naturalist, and I know many others.

Many of us naturalists now work in museums as taxonomists. That is, we spend our lives classifying animals. Darwin, incidentally, spent eight years on this kind of work, on a classification of the barnacles of the world, while he was writing the *Origin*, and it was an important part of his training. It is sometimes said that museum taxonomists work with the dead remains of animals and that we ought to turn to study of living things, but this is a dangerous half truth. It is true that living things are important and dead remains in themselves are not. What is not true is the implication that museum taxonomists are concerned only with dead remains. In fact, we study living animals through their remains. We still study evolution. I think Huxley has said that modern taxonomists are concerned with "detecting evolution at work." Geneticists and mathematicians can tell us how evolution seems to work or how it ought to work, and this is very important, but naturalists and taxonomists see how it has worked and does work. Among persons who, at least partly as naturalists and taxonomists, have made notable contributions to understanding of evolution in the last few years are Dr. Simpson and Dr. Mayr, who are contributing to this Darwin celebration. Need I add that man has been produced by evolution and is still evolving and that understanding evolution is a vital matter? Two vital and practical questions that naturalists and taxonomists can answer better than laboratory evolutionists are, how fast does evolution really go in animals (including man), and what happens in the course of time when death rates are reduced or populations isolated so that competition and selective pressures are reduced (as they have been in man)? So it is not a question of whether it is more important to study living animals or dead ones; we have to study both; study of dead remains can tell us things about life that we cannot learn in any other way.

Darwin, as a naturalist, was interested in everything around him, from beetles to geology; that (and luck) got him his place on the *Beagle;* and his background as a naturalist and collector and taxonomist enabled him to see and finally to interpret the patterns made by evolution when he found them clearly marked in South America and the Galapagos.

But why was Darwin a naturalist? From his short autobiography (3: 16, 17, 20, 27) we learn that he was an "ordinary" student, "singularly incapable of mastering any language," slow in mathematics (". . . I do not believe that I should ever have succeeded [in mathematics] beyond a very low grade"), and handicapped by "my incapacity to draw . . . an irremediable evil." On the other hand the "passion for collecting which leads a man to be a systematic naturalist, a virtuoso, or a miser" was very strong in Darwin and "clearly innate" (3: 13–14). He was identifying plants and collecting "all sorts of things, shells, seals, franks, coins, and minerals" by the time he was eight years old (3: 13), and he repeatedly refers to his "passion," "zeal," and "excitement" in natural history, which lasted all his life. From this we may deduce an inborn intensity of interest and power of concentration. To these driving qualities he added a need for explanations. This combination of weakness in language, mathematics, and drawing, more than balanced by intensity of interest and power of concentration, is characteristic of many naturalists and many good biologists, I think. Of course there are individual variations. Some biologists, fortunately, are good at mathematics.

Nora Barlow, his granddaughter, sums Darwin up thus (4: 157–158): "The love of close observation of natural fact and his need for a theory to explain everything he saw, forms the closely woven tissue which constituted his genius." This is true, but it is not much more than saying, in different words, that he was a good, serious naturalist. I suppose he was born with the capacity and that his training and experience developed it. But why are men born like that?

Darwin had one characteristic that many naturalists lack and that may take us one more step toward understanding him. He never hurried if he could avoid it. I do not know whether the reason was patience or caution or lack of confidence; perhaps a combination. Whatever the reason, he habitually took his time, went over and over and over the evidence, criticized his own ideas over and over and over again, before he was ready to publish conclusions. His own description of how he wrote *The Origin of Species* is famous. He got clearly on the track of evolution in South America and the Galapagos in 1835. Then, to quote from the introduction of the *Origin* (2: 1),

> On my return home, it occurred to me, in 1837, that something might perhaps be made out on this question by patiently accumulating and reflecting on all sorts of facts which could possibly have any bearing on it. After five years' work [in 1842] I allowed myself to speculate on the subject, and drew up some short notes; these I enlarged in 1844 into a sketch of the conclusions, which then seemed to me probable: from that period to the present day [1859] I have steadily pursued the same object.

This passage from the *Origin* helps to explain why Darwin not only discovered evolution but proved it. And I think it accounts for his zoogeography, which (as I have said) may be a better measure of his capacity than the discovery of evolution. Consider the pressure of the times. He saw and accepted a revolution in geological thought. He made a revolution in biological thought. Stupendous new ideas surged over him. But he never let them push him too fast or too far. He saw the effect of the ice age on animal distribution (how it left arctic plants and insects on mountain tops) before Forbes did, but Forbes published it and (properly) got the credit, while Darwin waited. But Forbes, I suppose under the pressure of the times, also propounded a series of stupendous (and, as we now know, impossible) land bridges, while Darwin waited. Finally, as part of his abstract on evolution, Darwin carefully laid down general principles of the relation of evolution to animal distribution, accepted great changes of climate and of land up to a point, but decided that the evidence did not authorize vast recent changes in the position or connections of the continents. He waited, collected and considered evidence, and criticized and revised his ideas, until he was right.

I want to make one more point and one more digression. It was part of Darwin's good fortune to have enough time. He was still in his teens when he learned that he would be at least a fairly rich man (3: 19). This took some of the force out of his efforts to prepare for medicine or the church (he considered first one and then the other), but the family money gave him time to go as unpaid naturalist on the *Beagle*, and later it allowed him time to work in his own unhurried, very careful, self-critical way. If Darwin had not had much time, he might have accomplished nothing. I wonder whether, in educating biologists, we value time highly enough now? We hear a lot about advanced placement and accelerated programs for superior students, and they may be good things for undergraduates. But post-graduate work ought to be entirely different. It should never be accelerated, at least not in biology. The years of graduate study may be the only period in a biologist's life when he has (or should have) time to do research of his own choosing in his own way. He should have time to accumulate evidence, speculate on it, sketch tentative conclusions, try them and reject them and draw new conclusions, and keep on until he is right, or at least until he has satisfied himself. If he does not have time, he may never learn self-criticism. He may accomplish nothing, or he may be hurried into publishing something half done and incorrect, which he may waste his life defending. Some educators realize this. Harvard's junior fellowships are designed to give young men three years of uncluttered time, the kind of time Darwin had.

All this does not really explain Darwin, of course. I do not know why he was the kind of man he was—a close observer of the things around him, who needed to explain what he saw. But, being that kind of man, he accomplished what he did because he lived in the right generation, became a naturalist, went on the *Beagle*, never hurried, and had the time he needed.

This paper of mine on Darwin and Zoogeography contains nothing new. It is just parts of a well-known story arranged around a new theme. In conclusion I want to say that zoogeography is a complex subject and Darwin was a complex man. What I have said has had to be oversimplified, but I have tried to keep it true as I simplified it.

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